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THE BIONOMICS OF *LAMPRONIA RUBIELLA* (BJERKANDER), THE RASPBERRY MOTH, IN SCOTLAND

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SYNOPSIS.

The raspberry moth causes serious damage to cultivated raspberries during certain years, particularly in the Scottish fruit-growing areas where it is a major pest. In the south of England it is less abundant, although in recent years there have been indications that it may become more widespread and plentiful there (Massee, 1939, 1942, 1946).

The female moth lays eggs during June and July in the fleshy tissue at the base of the corolla and androecium. The larva, on hatching from the egg, feeds for a short time on the surface tissue of the developing fruitlet, but within a few days it penetrates into the fruit to feed on the fleshy receptacle. During this period it casts its skin once. From the fruit the second instar larva migrates in search of a place in which to hibernate. Hibernacula appear to be situated mostly in the soil close to the roots of the raspberry plants. Prior to hibernation taking place, the larva moults for the second time, so that it passes the winter as a third instar larva.

With the approach of spring, at the time when the raspberry buds are bursting, the larva leaves its hibernaculum and crawls up a cane until it finds a suitable bud into which it eats a tunnel through the closely packed leaflets. Sometimes a larva, after having consumed the contents of its first bud, leaves it and attacks a second bud which, by this time, may have developed into a young lateral two to three inches long. The larva, which infests a single bud during its spring life, pupates in that bud, but that which infests more than one bud pupates on tie-wires, leaves, canes, supporting posts or similar places. During its spring life the larva passes through another two instars (the fourth and fifth) before pupating.

The full-grown larva prepares for pupation by spinning a white silk cocoon in some suitable place. This takes approximately five days to complete. Within the cocoon the larva pupates and the pupa remains for a period of three weeks.

Adult moths appear in June and are abundant during the second half of the month. Egg-laying then commences and a new generation of the species begins.

The summer larvae, which hatch during July from eggs laid in the flowers by the female moths, do little damage to the fruit because they are very small and their feeding is largely confined to the receptacle tissue.

The most serious damage is perpetrated by the larvae which emerge from hibernation in early spring and bore into the developing buds and laterals. Although their primary buds are killed by the caterpillars these are usually replaced by secondary buds; if these in their turn are largely destroyed by migrating caterpillars the plant's recovery is prevented because there are no further replacements to overcome the second wave of attack.

INTRODUCTION.

In the eastern area of Scotland (Angus, Perthshire and Fife), the raspberry moth *Lampronia rubiella* (Bjerkander) is one of the most serious pests in raspberry plantations. The plants are damaged only by the larval stage, which is known to growers as the "Borer".

It occurs in all parts of the fruit-growing region and is locally abundant during most years; from time to time serious infestations occur simultaneously on almost every fruit farm. Experienced growers have expressed the view that there are heavy infestations at intervals of approximately nine years.

The last serious outbreak in the area occurred in the spring of 1945, when fields which normally would have been green looked quite bare, the canes being almost

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defoliated by the caterpillars of *L. rubiella*. In some places, 90 per cent. to 100 per cent. of the buds were attacked. Cameron (1945), writing of that outbreak stated: "On one Scottish plantation . . . the infestation was such as to average fifteen caterpillars per cane at the rate of one per bud." Ormerod (1898) also makes mention of heavy outbreaks in England, for instance, "from ten to fifteen acres being so badly damaged that they looked as if it might be the middle of winter".

Fortunately, the plants are able to make some measure of recovery, even from such heavy attacks, by sending out secondary lateral branches later in the season to replace the damaged buds so that, by the end of the summer, some fruit is available for picking. Not infrequently, as described later, these secondary laterals are also attacked and when this happens the fruit bushes are unable to make good the loss caused by the first wave of infestation.

THE DISTRIBUTION OF *LAMPRONIA RUBIELLA* (BJERK.).

Meyrick states that, outside Britain, *L. rubiella* is present in northern and central Europe and Asia Minor.

Within the British Isles, *L. rubiella* occurs wherever raspberries are cultivated on a field scale. Meyrick (1928) gives the following details: "Britain to the Clyde, Ireland, common." Long before that date, however, the raspberry moth had been found in parts of Scotland north of the Clyde Valley latitude (for example, a correspondent of E. A. Ormerod reported its presence in the Crieffi district of Perthshire in 1891) and it now seems that it is a pest of much more general importance in the Scottish raspberry-growing areas than in Sussex and Kent, for instance, although according to Massee (1945), ". . . it appears to be increasing in the south of England".

In the east of Scotland, wild forms of *Rubus* such as *Rubus idaeus* L. (wild raspberry) and *Rubus fruticosus* L. (wild bramble), although certainly not immune, do not seem to be so severely attacked by *L. rubiella* as are cultivated raspberries. Nevertheless, they do form a reservoir where the insects can breed and from which they spread to cultivated raspberries growing nearby.

In Holland, where raspberry growing is an important industry and *L. rubiella* a serious pest, pioneer work on its control has been carried out. In North America, the first report of *L. rubiella* came in the spring of 1936, when larvae were found infesting raspberry plants in a plantation near Fredericton, New Brunswick, Canada. Within three years other infestations had been reported from Keswick and Kingston along the St. John River valley, and also at Prince Edward Island. Wild raspberries growing by the wayside were also attacked. Since its first appearance in Canada it has spread considerably (Maxwell and Lord, 1939).

GENERAL NOTE ON METHODS ADOPTED IN STUDYING THE LIFE CYCLE OF *LAMPRONIA RUBIELLA* (BJERK.).

The raspberry moth is a difficult subject for investigation because much of its life-history is passed within a bud or in the soil. When removed from their natural habitat the larvae do not feed and invariably die within a few days but it is comparatively easy to rear larvae by artificially infesting growing buds; much use was made of this method to supplement critical observations on the life-history of the moth made in the field.

THE EGG.

Oviposition.

Although numerous attempts were made to induce gravid female moths in captivity to lay on raspberry flowers none was successful. The female moths often evinced much interest in the flowers, but were never observed to lay eggs.

When the adult moths were introduced into the cages they fluttered about in an excited manner, alighting after a brief period on the flowers but continuing to move rapidly, pushing their heads downward to the bases of the petals and stamens and also exploring the receptacle region with the tips of their abdomens.

When a female appeared to have found a suitable flower she supported herself by clinging to the stamens; she then extended her abdomen until its tip touched the receptacle at the bases of the petals. Rhythmic contractions of the abdomen followed and the small ovipositor could be seen moving out and in so that the receptacle tissue just outside the stamen bases, with which it came in contact, was pierced.

While the moth was so engaged, the wings were held in a horizontal position (i.e. relative to the vertically placed body of the insect) away from the dorsal surface of the abdomen and slightly open. Suddenly the wings were depressed to their normal position over the moth's back and within a few seconds of this happening the moth left the flower. The whole process from the commencement of "probing" with the ovipositor to leaving the flower, occupied one and a half minutes. The actual deposition of eggs was not seen in any of the specimens kept under observation.

Chapman (1891) described briefly the oviposition of *L. rubiella* and gave two and a half minutes as the time taken for the complete operation. Thus the observations just described were not, in all probability, of complete sets of oviposition but of unsuccessful attempts. The fact that subsequent examination of the flowers revealed no eggs confirms this.

Lundblad (1934) stated that "the eggs are laid in the open blossoms immediately on the stamens". He probably mistook the eggs of *Byturus tomentosus* F., the raspberry beetle, for those of *L. rubiella*.

Egg-laying takes place during the last two weeks of June and is completed by the first week of July. During that period large numbers of raspberry flowers, collected in a plantation where *L. rubiella* was known to be present, were examined for the presence of eggs. In many of the flowers small brown points of bruised tissue were seen at the junction of the calyx and the receptacle. On dissection, only a few of these spots were found to contain small colourless eggs situated just below the surface of the receptacle.

Description.

The egg was briefly described by Chapman (*loc. cit.*) but no measurements were given. The description which follows here is based upon examination of eggs obtained as outlined above.

The egg is colourless and semi-transparent, with a smooth, shining unsculptured surface. It is oval in shape, being broadest near the middle and tapering at each end. Its greatest breadth is approximately two-thirds of its greatest length. The following are the means of measurements of the few eggs found:

Average length: 0.35 mm. Average breadth: 0.21 mm.

THE LARVA.

Method of study of spring larval growth.

Exact data could not be obtained about the duration of the several larval stages or instars, owing to the difficulty of keeping the larvae under direct observation. Consequently, approximate periods were estimated by indirect methods.

This was done by visiting a plantation every three days and collecting infested buds which were examined individually in the laboratory. The sizes of the larvae in the buds were noted. When a larva appeared to be distinctly larger than the majority of its fellows, search was made for an empty head capsule in the bud among the frass and debris as evidence of ecdysis having taken place. Lengths of instars were therefore standardized as accurately as possible from the first appearance of spring larvae, the first discovery in a bud of one head capsule, the first discovery in a bud of two head capsules, and the first appearance of a non-feeding larva.

As visits were made regularly and frequently to the plantation and many buds were collected and examined after each visit, the record of the growth-rate of the spring larvae of *L. rubiella* so obtained is probably a good approximation to the facts.

Description of larval stages.

First instar larva. The newly hatched larva of *L. rubiella* is quite colourless except for the head capsule, which is pigmented. As it hatches, its dark head capsule can be seen clearly in the plant tissue. At eclosion the larva measures approximately 0.72 mm. in length. The duration of the first stadium is about ten days.

Second instar larva. After the first ecdysis the larva is again almost colourless except for the head, a dark pronotal plate, plates on the last segment of the abdomen, and the dark segments of the legs. The body, dorsal to the mid-lateral lines, shows a faint pink tinge. Ventrally, the larva is colourless. Its length is 2.95 mm. approximately, but nine days later this increases to 3.83 mm., approximately, and the larva is ready to leave the fruit and migrate in search of a suitable site for hibernation. The red pigmentation is much more marked, especially dorsally. The ventral region of the larva is light cream to orange. On the abdominal segments, distinct double mid-dorsal lines are visible. These are of a rather deeper red colour than the surrounding tissues and are separated from each other by a narrow yellow line. These lines are absent from the thoracic segments and are not distinctly visible on larvae of later instars.

Third instar larva. After leaving the raspberry plant and having prepared for hibernation, the larva casts its skin once more and passes the winter as a third instar larva.

Specimens of larvae, which can be washed and sieved from soil samples during the winter, are red in colour except for the head, the legs, pronotal plate and plates on the last abdominal segments. This appearance is maintained until the larva is ready to migrate to the buds in early spring at which time it measures 4.13 mm., approximately, in length. After the bud is attacked, a further ten or eleven days elapse before ecdysis takes place and the fourth instar larva appears.

Fourth instar larva. In general form and colour, the fourth instar larva is identical with the third. Its maximum length is 6.78 mm., approximately. The duration of this stadium is about fourteen days.

Fifth instar larva. The final larval instar lasts for about fourteen days, of which the last five days are sometimes spent by the larvae in migrating to suitable pupation sites and in spinning cocoons.

In appearance, the feeding stage of the fifth instar larva resembles the fourth. It is bright red, with black head, legs, pronotal plate and plates on the last abdominal segment. When fully grown, it measures 7.77 mm., approximately, in length.

When it has completed feeding, the larva prepares to pupate and begins to spin its cocoon. During the non-feeding period which lasts four to five days, the body of the larva shrinks somewhat, the segments becoming slightly telescoped into each other.

Seasonal behaviour of the larvae.

(a) *Late summer.* The larva hatching from the egg at the beginning of July makes its way to the receptacle of the fruit, entering by the narrow spaces between the green drupelets. The young fruit is scarcely damaged by the feeding of the larva and appears quite normal to the unaided eye. The presence of small pellets of frass near the base of the berry is usually the first indication that a larva is within. Under the microscope, the surfaces of the basal drupelets next to the receptacle are seen to have had shallow grooves gnawed in them and small pellets of excrement are again present. When the fruit is ripe, it is undamaged except for the somewhat dry appearance of some of these affected drupelets.

After a few days, the larva ceases to feed on the drupelets and moves to the fleshy receptacle where it eats a groove round the receptacle and towards the tip.

When the fruit is picked, the larva is not usually removed with it, but, sheltered within its groove, remains for some time—usually for not more than two days. It then begins its migration in search of a place in which to hibernate. By this time the larva has grown in length to about 3.8 mm. and is already quite red dorsally. Some previous investigators have described the late summer larva as being white or colourless. This is not so, for, although it is colourless at first, it assumes a brilliant red hue before it leaves the fruit or receptacle to migrate to the soil. The red coloration, however, is not so uniform or so deep in hue as that of the spring larva.

More than one larva of *L. rubiella* was never found in one fruit, although occasionally it was accompanied by a larva of the raspberry beetle (*Byturus tomentosus* Fab.). However, more than one larva may possibly share a fruit because a flower was once found containing two eggs. Beirne (1943) records that "Normally only a single larva is found in each infested fruit, but in two cases two larvae were found, probably from eggs laid by different females".

(b) *The larval migration to the soil in late summer.* To assist in studying the late summer migration of the larvae from the fruit receptacles to their hibernacula, grease bands 6 inches wide were painted on canes 6 inches above the surface of the soil, to trap the larvae migrating down the canes. At the same time the foliage was beaten to dislodge any larvae crawling on the laterals.

Both methods showed that the late summer migration of larvae occurs during a period extending from about the second week of August until the end of that month.

(c) *The location of hibernacula.* As most of the control measures at present in use against *L. rubiella* involve the application of insecticides to the soil, in which the larvae pass the winter, it is important to know accurately where the hibernacula are.*

Chapman (1891) stated: "On its escape (from the fruit) it no doubt proceeds to the base of the stem in the 'stool' of the plant and passes the winter." Ormerod (1898) merely quoted Chapman's remarks. Theobald (1909) added that "the usual position is either under the rough rind of the canes or in cracks and crevices of the stalks; they also occur under stones or pieces of wood lying about in the plantations". In the discussion which followed Harris' paper (1935), statements about the hibernation of *Lampronia* larvae were made by two growers. Both indicated that stumps or "snags", left after the old raspberry canes had been cut out, provided shelter for the larvae. Maxwell and Lord (1939), while investigating the life-cycle of the raspberry moth in Canada, attempted to locate the winter cocoons, but were unsuccessful. Massee's statement (1945) more or less agrees with that of Theobald.

To discover the situation of hibernacula, extensive soil samplings were made during the winter. Cores of soil, 4 inches in diameter and 9 inches deep, were taken by means of a cylindrical sampler. The main object was to discover whether the winter cocoons were (a) in the soil among the roots of the raspberry plants, or (b), in the alley-way between the rows. The apparatus used for washing the soil samples was a slightly modified version of that described by Salt and Hollick (1944).

Although many other insects and insect larvae, often quite as small as the larva of the raspberry moth, were successfully recovered from the soil samples, no larvae of *L. rubiella* were obtained.

When soil washing failed to yield any hibernating larvae, some hundreds of old cane-bases or snags were brought to the laboratory and thoroughly examined. Again, numerous specimens of insects, including many specimens of the larval stage of *Ametastegia glabrata* Fall. (the dock sawfly), were located in the snags but no cocoons of *L. rubiella* were obtained. Thus the growers' views noted earlier (Harris, 1935) that old stumps harbour *L. rubiella* larvae, do not seem to have been well founded and other insect larvae were possibly mistaken for the "borer".

Observations made previously seemed to indicate that the larvae might hibernate in the soil actually within the stool near the roots. To test this idea, a large number of stools was obtained from an infested field which was being "grubbed up". In the laboratory the soil was shaken and beaten from the roots and washed through sieves. The roots were then placed in the top tray of the soil washing machine and were thoroughly washed with strong jets of water, so that no particles of soil remained on them; the roots and canes were carefully examined. No larvae were found on the roots or canes or in the debris trapped between the canes, but four larvae were recovered from the sieved and washed soil.

As the total quantity of soil washed from the roots of the old stools was much less than that in the soil cores, it seems justifiable to conclude that, had larvae been

* An account of the author's experiments on the control of the raspberry moth will be published shortly.

present in the latter, they would certainly have been recovered. Their brilliant red colour makes them conspicuous and readily detected if present.

It is concluded, therefore, that while some of the over-wintering larvae may hibernate in slits in canes and supporting posts and in debris, most of them hibernate in the soil close to the roots of the raspberry plants.

(d) *The spring emergence of larvae.* The time at which the larvae emerge from hibernation in spring varies according to the climatic conditions. Thus, in the spring of 1946, which was regarded as a normal season, larvae in numbers were first noticed climbing up the canes on 6th April. In 1947, after a long and severe winter, the first larva was detected on 12th April, but it was not until 16th April that the presence of larvae became obvious. One grower supplied information that in 1945 the larvae appeared as early as 22nd March. In that year the infestations of *L. rubiella* were exceptionally severe.

In order to plot out the period of emergence of spring larvae, regular visits were paid to a plantation of Norfolk Giant raspberries which was known to be infested.

In this plantation 154 canes, chosen at random during the first visit, were labelled and numbered. Frequent visits were then made when all the buds on the 154 canes were examined. Any infested buds were cut off, so that after each visit the 154 canes were left free of infestation and, therefore, any buds showing "primary" infestation discovered during the next visit must have become infested in the intervening period of time. The data are set out in Table I.

TABLE I.

Emergence of Larvae on 154 canes of Norfolk Giant Raspberry in 1947.

Date 1947.	Number of infested buds.
12th April	1
16th ,,	16
22nd ,,	344
24th ,,	55
28th ,,	64
1st May	52
5th ,,	10
8th ,,	4
12th ,,	0

Thus the period in spring when the larvae were migrating from their hibernacula to the buds was a protracted one lasting about a month. Most larvae, however, emerged during the two weeks, 16th April to 1st May, with the peak emergence on 22nd April. Thereafter fewer and fewer larvae emerged and after 12th May no new infestations were found.

The observations made on the spring emergence of larvae and the ensuing infestation of raspberry buds lend no support to the theory, widely entertained by growers, that the larvae eat their way up the inside of the cane in order to reach the buds, as do larvae of the closely related currant shoot borer, *Lampronia capitella*

Clerck. The larvae begin to cause damage when they start feeding on the outsides of the bursting buds which they have reached by climbing up the surface of the cane.

Having found a suitable bud, the larva begins to eat its way into it, forming a tunnel which at first is narrow. Within an hour of commencing to feed, the larva has disappeared within the bud, leaving a small quantity of frass at the opening of its tunnel. Inside the bud the larva continues feeding on the young leaves which remain unexpanded in consequence. The tunnel is widened and extended until the pith of the cane is reached. Within the tunnel, frass accumulates and is usually loosely held together by fine strands of silk, spun by the larva. After the larva has moulted, old head capsules are to be found amongst this frass. Some larvae pass the whole of their spring feeding period in one bud and finally pupate there ; others behave differently.

Observations on the habit of L. rubiella larvae of infesting more than one bud.

About a fortnight after the first appearance of the larvae in spring, some attacked but unoccupied buds are to be found. At this early date no pupae are present in the field, so the emptiness of the buds cannot be due to their occupants having left them to go elsewhere to pupate—pupae are not normally found until two or three weeks later. One explanation for the empty buds is afforded by the appearance of fourth and (later) fifth instar larvae making fresh attacks on young laterals. These larvae, having "eaten out" their original buds (which will henceforth be referred to as "first buds") wander to other buds or developing laterals ("second buds" or "second laterals") which they attack and destroy.

Such "secondary" attacks can be the cause of serious trouble ; for example, the plant, after having suffered the primary attacks of the larvae, seeks to recover by developing secondary laterals. If, however, these secondary laterals are in turn attacked by wandering, partly-grown larvae, the plant's chances of recovery are materially reduced.

This habit of the larvae of leaving the buds damaged in the primary attacks and of wandering to other buds and to developing laterals has been known for many years (Ormerod, 1898).

PUPA,

Site of pupation.

When the larva is full-grown it prepares to pupate. The site chosen for pupation varies. Some larvae remain in the buds in which they have been feeding since leaving their hibernacula. Others leave the shelter of their buds and wander over the plant to pupate on the upper surfaces of leaves and petioles and occasionally on their under surfaces, the surfaces of the canes, on tie-wires and supporting posts. It was often noticed that the upper surfaces of leaves and petioles were more favoured by larvae than the lower surfaces. Pupae have never been found in the soil.

The prepupal period.

Having arrived at a suitable site, the larva spins a cocoon. This cocoon is of white silk and at first is thin-walled. Cocoons found on leaves have usually been spun in the form of a small sheet on the flat upper surfaces of the leaves, although once the insect had stitched the leaf over itself, forming a small chamber, like some members of the Tortricidae. Larvae which had infested second buds or laterals

were frequently found spinning cocoons on the leaflets of these buds. Occasionally, elongate silk cocoons were found on the wires which support the canes.

Larvae ready to pupate begin to appear during the second week of May, but specimens are to be seen spinning their cocoons as late as the end of that month.

The larva takes four days to construct its cocoon. During the first day it covers itself completely with a sheet of silk which is of a fine texture and semi-transparent. During the remainder of the spinning period it continues to add

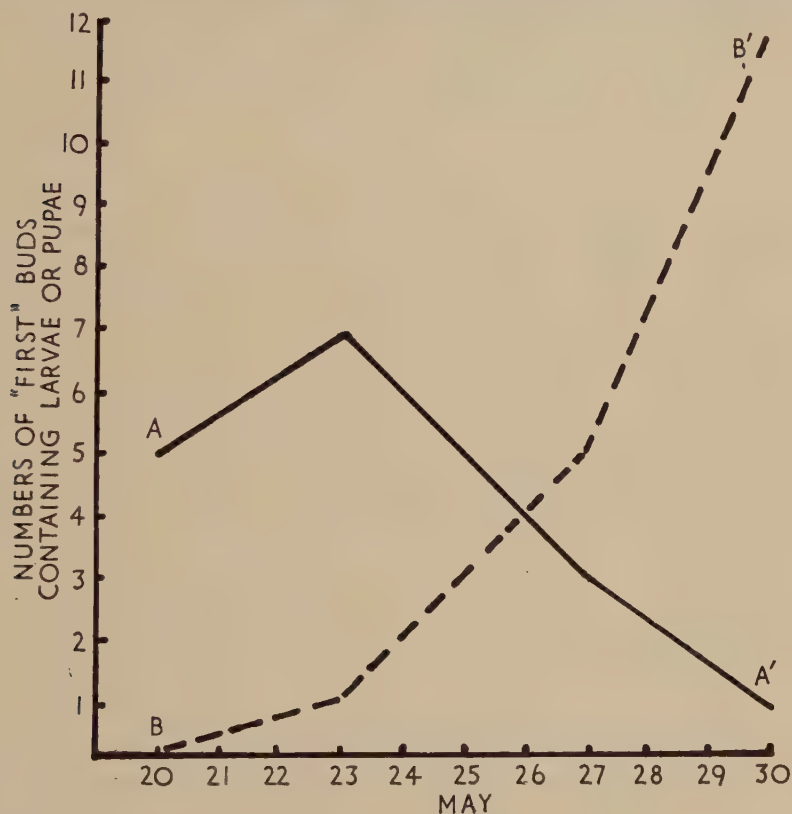


FIG. 1.

Numbers of Larvae and Pupae found in "first" buds on each of four days between May 20th-30th, 1947. A—A' = Larvae. B—B' = Pupae.

strands of silk until the walls of the cocoon are so dense that the occupant is barely visible inside.

The final larval ecdysis occurs within 24 hours of the cocoon having been completed.

To investigate the reason for the differences of behaviour referred to above, canes were chosen at random during four visits to a plantation and every bud on each cane was examined to ascertain whether they contained larvae or pupae, or were empty; whether the buds were "first" or "second" buds was also recorded. The results of these observations are shown in Figures 1 and 2.

In Figure 1, the curve AA' represents the total number of larvae found in "first" buds on each of four visits to the plantation made between the 20th and the 30th of May. Generally the curve shows an even and continual decrease in the number of larvae in "first" buds. Such a decrease might have been due to the larvae having (a) left the buds to pupate elsewhere, or (b), remained in the buds and pupated, thus becoming unrecordable as larvae.

The curve BB' represents the pupae present in "first" buds on each of the four visits and shows that the latter explanation is the correct one, as the numbers of pupae in "first" buds increase as the larvae decrease.

It seems safe, therefore, to conclude that a larva which passes its entire spring larval life in a single bud remains in that bud to pupate.

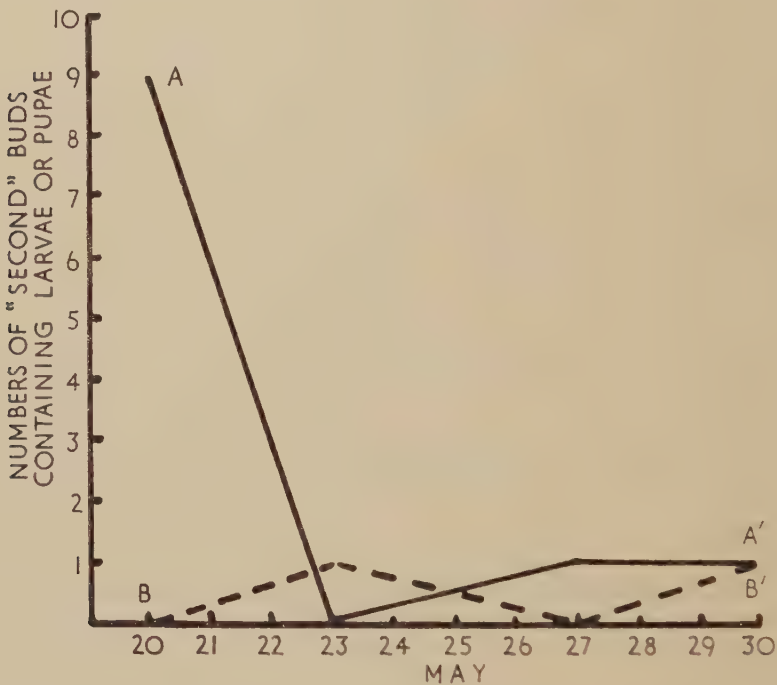


FIG. 2.

Numbers of Larvae and Pupae found in "second" buds on each of four days between May 20th-30th, 1947. A—A' = Larvae. B—B' = Pupae.

Figure 2 shows that the numbers of larvae in "second" buds during the ten days from 20th May to 30th May drop markedly. This again could be due to the causes (a) and (b) suggested above.

If the second were true, then the numbers of pupae present in "second" buds should rise as the numbers of larvae fall. The curve BB' does not bear this out, for the numbers of pupae found in "second" buds are very small and never increase by amounts comparable with the fall in the numbers of larvae in "second" buds.

Thus it appears that the larvae which attack more than one bud during their spring feeding period also leave the "second" buds and pupate elsewhere outside the buds, as described above.

To summarize, there appear to be two clear-cut behaviour patterns displayed by the spring larvae of the raspberry moth. In the group displaying the first type are larvae which pass their entire spring feeding-period in the bud which they first infest after leaving their hibernacula. These larvae also spin their cocoons and pupate, each within its bud. In the group displaying the second type, the larvae leave their original buds and laterals, causing further serious damage. When these larvae are full-grown they leave their "second" buds or laterals and spin their cocoons in situations such as the surfaces of leaves and canes, or tie-wires and supporting posts.

Description of the pupa.

Immediately after final larval ecdysis, the pupa is of the same red colour as was the larva. One day later it becomes brownish red and, in three days' time, changes to a deep brown colour with only a trace of red.

The pupal skin is smooth and shining and the eyes, antennae, proboscis and wings are clearly visible. Westwood (1853) remarked that the proboscis is rolled spirally instead of lying flat on the ventral surface of the thorax.

Dorsally, the first seven abdominal segments are each provided with a transverse row of small bristles placed at the anterior third region. The penultimate abdominal segment bears two small but stout hooks which serve to hold the pupal skin fast within the cocoon as the imago struggles to emerge from it. The average length of the pupa is 5.2 mm.

The duration of the pupal period.

Field observations showed that the pupal period lasts for about three weeks. In 1947, for instance, when it was possible to make an unbroken series of observations, the first pupa was found under field conditions on 27th May and the first adult moth appeared 21 days later.

The emergence of the adult.

Prior to emergence, the pupa pushes its way out at the head-end of the cocoon so that the fore-part of the body projects beyond the cocoon or, if pupation has occurred in a bud, beyond the opening of the tunnel or boring. The pupal skin splits dorsally at the anterior end and the adult moth struggles free, leaving the empty husk-like pupal skin projecting from bud or cocoon.

THE IMAGO.

The time of appearance of the first imago varies from year to year. During the first week, only a few imagines are to be seen but, about 14 days later, their numbers are greatly increased and the peak of emergence is reached. The moths are then frequently to be seen flying during the day and especially in warm sunny weather. After another week, their numbers diminish until, four weeks after the appearance of the first imago, no moths are to be found.

Description of the imago.

The imago of *Lampronia rubiella* (Bjerk.) is a small moth with an average wing-span of 11.6 mm. (see Fig. 3).

The head, which is light fawn in colour, is adorned with scales and erect and slightly backwardly curved bristles. The compound eyes are large. The antennae are filiform and in length are about one-quarter of the total length of the insect; they are provided with a fine pubescence. The mouth-parts are well developed and the labial palps are prominent. The prothorax is covered with dark brown to black scales.

The fore-wings are strikingly and beautifully marked. The ground colour is black, but the wings are ornamented with a number of yellow or golden spots of which two, situated on the dorsum, are large. Much smaller, yellow spots interrupt the costal margin and similar spots are dusted sparingly over the remainder of the wing. Apically, the fore-wings are fringed with long pale-tipped cilia.

The hind-wings, which are also fringed with long cilia, are of a uniform grey colour without any markings.

The legs are covered with light- and dark-coloured scales. The posterior pair of legs are longer than the other two pairs. The tarsi are well developed and consist of five segments of which the proximal one is extremely long.

The abdomen is covered with dull gold-coloured, elongate scales. Normally it is hidden under the wings which, at rest, are folded over it.

A PARASITE OF LAMPRONIA RUBIELLA (BJERK.).

While studying the bionomics of this species, one Hymenopterous parasite was bred from a larva. Mr. J. F. Perkins, of the British Museum (Nat. Hist.) identified it as *Horogenes exareolatus* Ratz., a member of the Ichneumonidae (Hill, 1950).

SUMMARY.

The economic importance of the raspberry moth, *Lampronia rubiella* (Bjerkander), and the damage it causes to the plants is described.

Detailed observations on its life-cycle and seasonal behaviour are given.

Descriptions of the egg, larval instars, pupa and adult are outlined and the occurrence of a Hymenopterous parasite mentioned.

ACKNOWLEDGMENTS.

This work was carried out under a grant from the Agricultural Research Council to whom acknowledgment is made.

The author also expresses his thanks to Dr. R. V. Harris, Dr. C. H. Cadman, Dr. A. M. Massee and to others who assisted in the preparation of this paper, together with Mr. S. Sandison for access to his raspberry plantations.

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PLATE I.



FIG. 3.
Lampronia rubiella (Bjerk.), Adult $\times 17$.

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BIOLOGY OF THE FRUIT TREE RED SPIDER MITE *METATETRANYCHUS ULMI* (KOCH) IN SOUTH-EAST ENGLAND

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INTRODUCTION.

FOR several years the Fruit Tree Red Spider Mite had been causing such serious damage in commercial orchards of the Eastern and South-Eastern counties of England that in 1943 a joint investigation into the life history and control of the mite was initiated by the Agricultural Research Council, the Pettar Society of Winter Wash Manufacturers and the Associated Fruit Growers of Essex. The work was undertaken by East Malling Research Station and carried out at the Field Laboratory, Great Braxted, Essex. This paper is the result of a detailed study of the life history of the Fruit Tree Red Spider Mite made in the course of these investigations during the years 1945-49.

It is only during the last 25 years that the mite has risen to importance as a pest of fruit orchards in this country. Theobald (1911) recorded a mite from apple which he regarded as a potential pest but which he was unable to identify further than that it was a species of *Tetranychus*, and was distinct from the Gooseberry Red Spider (*Bryobia praetiosa* Koch). It is almost certain that the mite in question was the Fruit Tree Red Spider Mite. The first British record of the mite, as a serious pest, was by Massee (1926).

Synonymy.

The Fruit Tree Red Spider Mite was first described by Koch in 1835 and placed in Dufor's genus *Tetranychus* as *Tetranychus ulmi*. In 1876 Canestrini and Fanzago, working in Italy, described a mite from rose and named it *Tetranychus pilosus*. A few years later, in 1885, Riley found a mite on orange and described it under the name *Penthelodes mytilaspidis*. Thus the specific names *ulmi*, *pilosus* and *mytilaspidis* have all been used for this mite, but it has been moved from one genus to another in recent years. Berlese named the genus *Oligonychus* as part of *Tetranychus* in 1886, and Hirst (1920) and other workers considered that *Tetranychus ulmi* Koch should be included. American acarologists on the other hand preferred the generic name *Paratetranychus* used by Zacher (1913) and until recently they had always used the specific name *pilosus*. Therefore, for many years the mite was known as *Paratetranychus pilosus* (C. & F.) on the American continent and in parts of Europe, while in other countries, including Great Britain, it was known as *Oligonychus ulmi* (Koch).

In 1931 Oudemans erected the genus *Metatetranychus* and assigned *Oligonychus ulmi* (Koch) to it. *Metatetranychus ulmi* (Koch) is now considered to be the valid name of the mite and is being accepted as such throughout the world. A full synonymy was set out by Geijskes (1939).

The mite described by Riley as *Penthалodes mytilaspidis* was probably the Citrus Red Spider but, until the work of McGregor and Newcomer in 1928, this was often confused with the true Fruit Tree Red Spider Mite. It is probable, therefore, that records of *Tetranychus (Penthалodes) mytilaspidis* (Riley) and *Paratetranychus (Tetranychus) citri* (McGregor) on deciduous fruit actually refer to what is now known as *Metatetranychus ulmi* (Koch). Similarly, references to this last species on citrus trees are probably records of the Citrus Red Spider.

Distribution.

Since this mite was first recorded in the middle of the nineteenth century it has occurred in all the fruit-growing areas of the world except South Africa. The absence of the mite from this country of the southern hemisphere is of great interest but there seems to be no adequate explanation. It has been recorded from all the other fruit-growing areas of the southern hemisphere, Australia, New Zealand and South America; yet in South Africa the Tetranychid pest of deciduous fruit trees is *Bryobia praetiosa* Koch, known there as the Brown Mite.

The range of latitude over which the mite is found is 30°-60° in the northern and the southern hemispheres. Mabry and Walton (1939) give a very full list of the countries from which they had records of the mite; the list includes twenty countries of the four continents, Europe, America, Asia and Australasia. Many of these records are comparatively recent, some possibly because the mite had been previously overlooked, others probably due to its dispersal in various ways by man. Probably the chief method of dispersal from one country to another and from one district to another is by means of winter eggs on root stocks (Cottier, 1934) and scion wood (Listo, Listo and Kanervo, 1939); the former is undoubtedly the more serious. There is also the slight possibility that the winter eggs laid on the fruit, when a severe infestation occurs, may hatch in the spring in a situation where the larvae could survive, but this seems unlikely.

In Great Britain the mite has been recorded from the principal fruit-growing areas, but it is in the south-east of the country, in Essex, Kent, Sussex, Surrey and, to a lesser extent, the adjacent counties that it is most serious as a pest. In the West Country and the Midlands, where most of the fruits are cyder apples, cooking apples and plums, it had not been considered a pest of economic importance. However, in recent years in these parts of England it has steadily increased and is now regarded as an important pest. The Clyde Valley in Scotland is another area in which the mite is becoming more troublesome.

FLUCTUATIONS OF MITE POPULATIONS.

In a paper which considers the effect of environment and orchard management on the fauna of an apple orchard as a whole, Pickett *et al.* (1946) state that the European Red Mite may become very numerous after the spraying season as a result of repression of natural control agents. This appears to be exactly what has happened in the commercial orchards of Essex and Kent. It therefore follows that an orchard, where no sprays are used and no pruning or cultivation carried out, should have no mite problem. Such a "derelict" orchard in Essex was kept under observation and although the Fruit Tree Red Spider Mite was always present in small numbers, it never increased seriously as it was always kept in check by the numerous predators present.

There are at least five factors acting singly and together in a complex way to influence mite populations and cause the violent fluctuations so often noticed in commercial orchards. These factors are (i) the number of generations, (ii) the action of the predator population, (iii) weather conditions, (iv) the spray programme and (v) the dispersal phase of the mite.

(i) *Number of generations.*

In a sprayed orchard where, in spring, there are only a few eggs, these will hatch and, by autumn, produce a large population. Cutright (1939) states that the mite has a high "biotic potential". At one locality, in January 1949, only four

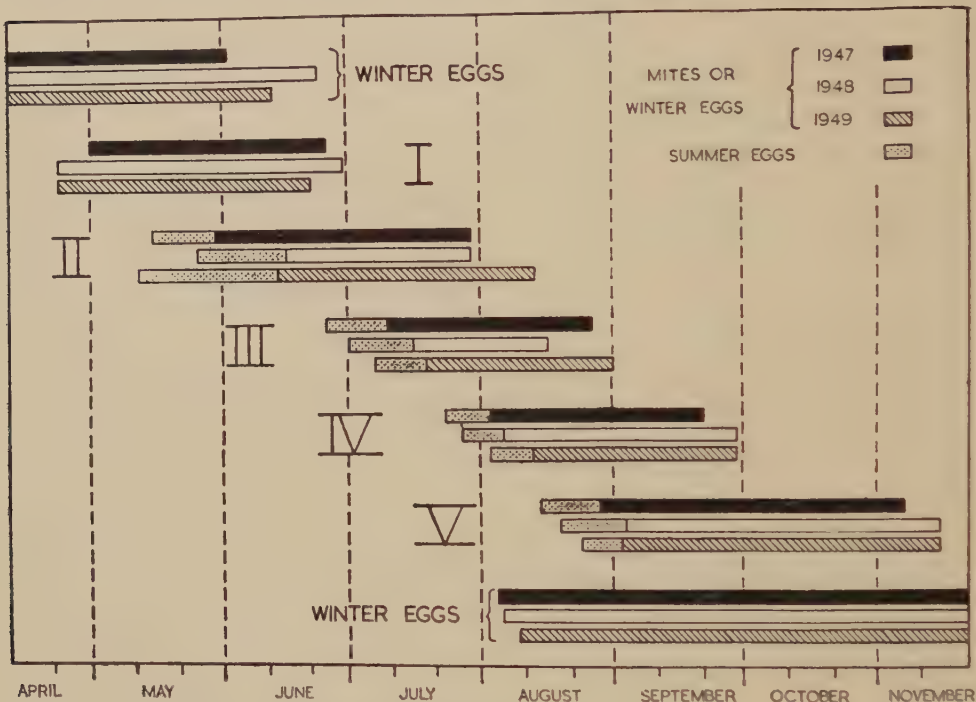


FIG. 1.

Fruit Tree Red Spider Mite, *Metatetranychus ulmi* (Koch), length and overlapping of generations, 1947-1949.

eggs could be found on ten apple shoots, but by November 1949, 1,273 eggs were found on the same number of shoots. This increase can be accounted for by the number of generations in that season.

In Essex and Kent it has been established that there are always five generations of the Fruit Tree Red Spider Mite in each season. Newcomer and Yothers (1929) give eight generations for the Pacific Northwest, Andersen (1948) five for Germany, Wiesmann (1940) five generations for Switzerland and Listo, Listo and Kanervo (1939) three to five for Finland.

Fig. 1 is compiled from field observations in Essex and shows the approximate length of each generation from the emergence of the first larva to the death of the

last adult in the first generation and from the laying of the first summer egg to the death of the last adult in generations two, three, four and five.

In 1948 the first generation larvae were still hatching from winter eggs when summer eggs, laid by early females of the first generation, were hatching on the leaves of the same trees to give second generation larvae. Two broods were therefore present from the middle of June onwards. In 1947 there was a slight overlap

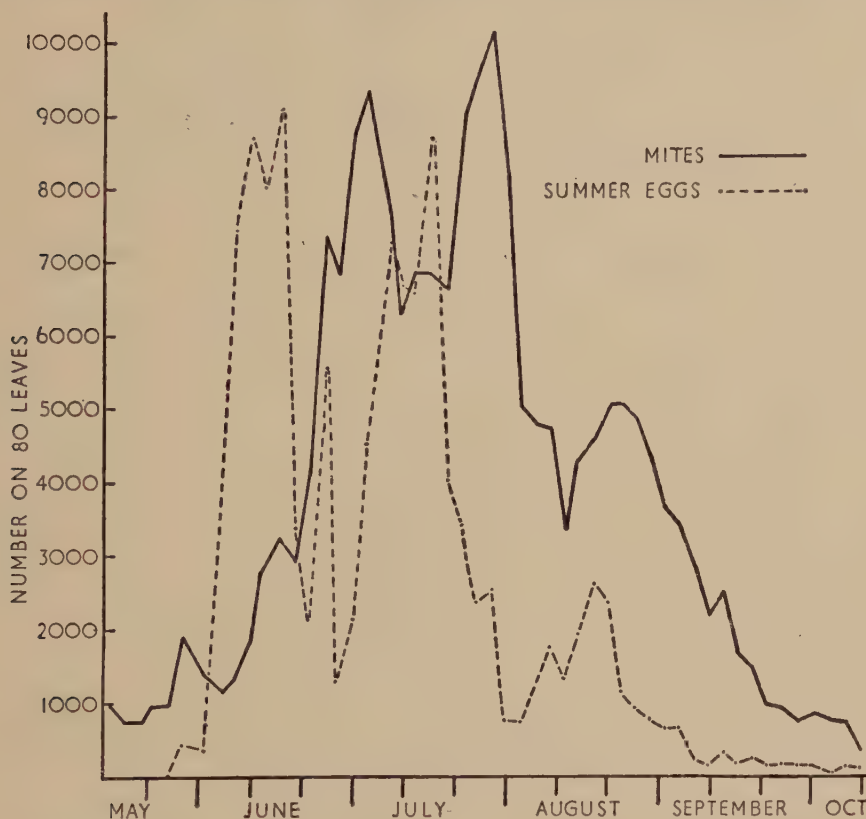


FIG. 2.

Fruit Tree Red Spider Mite, *Metatetranychus ulmi* (Koch), number of mites and summer eggs on 80 leaves during the summer of 1947.

of the first and second generations. Due to some unknown factor, the eggs laid by the first generation in 1949 had a long incubation period and larvae of the second generation were not present on the leaves while winter eggs were still hatching. Thus, in 1949, no overlap of generations one and two occurred.

Fig. 1 shows that not more than two generations were present at any one time on the leaves.

The dates of the laying of the first summer eggs in the years 1945-49 are shown in Table I. The first summer eggs were invariably found in that orchard where the first hatch of winter eggs occurred.

Throughout the work, when it was necessary to record population fluctuations, the "imprint method" (Austin & Massee, 1947) was used. Figs. 2-4 show the

TABLE I.

Comparative dates of the life history of the Fruit Tree Red Spider Mite.

Year.	1st hatch of winter eggs.	1st summer egg laid.	1st winter egg laid.
1945	17th April	7th May	27th July
1946	25th April	23rd May	22nd July
1947	30th April	19th May	1st August
1948	21st April	21st May	4th August
1949	21st April	23rd May	9th August

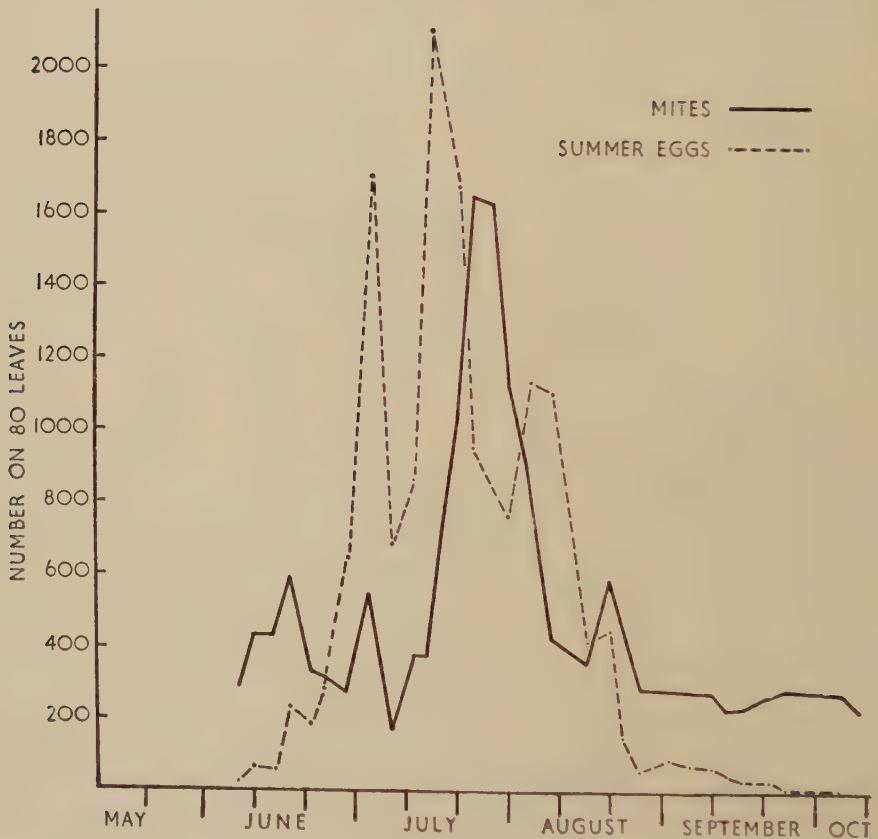


FIG. 3.

Fruit Tree Red Spider Mite, *Metatetranychus ulmi* (Koch), number of mites and summer eggs on 80 leaves during the summer of 1948.

number of mites and eggs on 80 leaves recorded by this method every third day throughout the three seasons.

The population built itself up during the first three generations and fell during the fourth and fifth, when some dispersal usually occurred and winter eggs were being laid. The fifth generation could not be clearly distinguished as it occurred when the population was dying out; also many mites were not recorded as they were on the wood, laying winter eggs. The population of active mites during the season was often greatly affected by predators during the later part of June, July and August, whereas the summer eggs rarely were; this can be seen in Fig. 3.

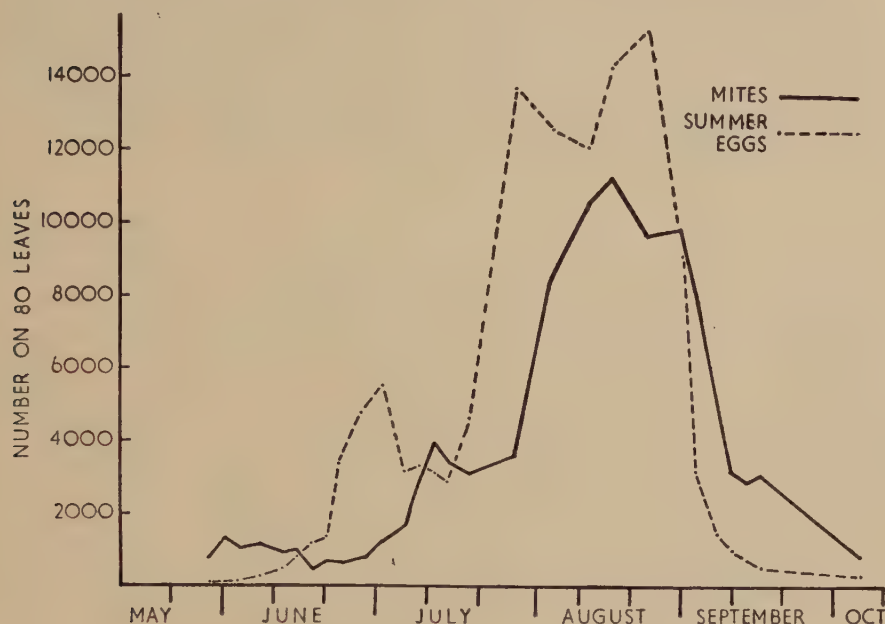


FIG. 4.

Fruit Tree Red Spider Mite, *Metatetranychus ulmi* (Koch), number of mites and summer eggs on 80 leaves during the summer of 1949.

Winter eggs were normally laid by the mites of the fourth and fifth generations but, in each year, some winter eggs were laid by the third generation. The dates when winter eggs were first recorded in each season are shown in Table I. In each year, winter eggs were found in most orchards within a fortnight of these dates but it was some time before they were found in great numbers.

Oviposition continued until cold weather killed the mites in November, or until leaf-fall. It was repeatedly noticed that in an orchard where a bad infestation occurred in July and the leaves were badly bronzed, females of the third generation laid winter eggs. In other orchards, winter eggs were deposited only by fourth and fifth generation females. While lack of food in some instances may cause a mite to lay winter eggs, there must be some other factor which induces this on trees which show no visible sign of damage.

The third and fourth generation mites laid both summer and winter eggs and it was shown that individual females can lay both types of eggs.

(ii) *Action of the predator population.*

Predators are one of the chief agents in reducing mite populations (Collyer, 1949). Unfortunately, many of the sprays which reduce the numbers of mites also kill large numbers of predators. Although these sprays may initially reduce the mite population, a few mites always escape and, in the absence of predators, the population rapidly builds up again. A detailed study of the effect of the predators in the autumn on the winter egg population was made (Fig. 5). Shoots were cut from ten trees and counts were made as described by Austin and Massee (1947). The percentage of eggs which were apparently normal, i.e. those showing a deep red colour, varied as the autumn progressed. The percentage of red eggs resulting from laying and sucking of the eggs on the wood is shown by the line of the graph. The graph starts in August with a certain percentage of red eggs, continues through September and the beginning of October with two definite peaks when many more

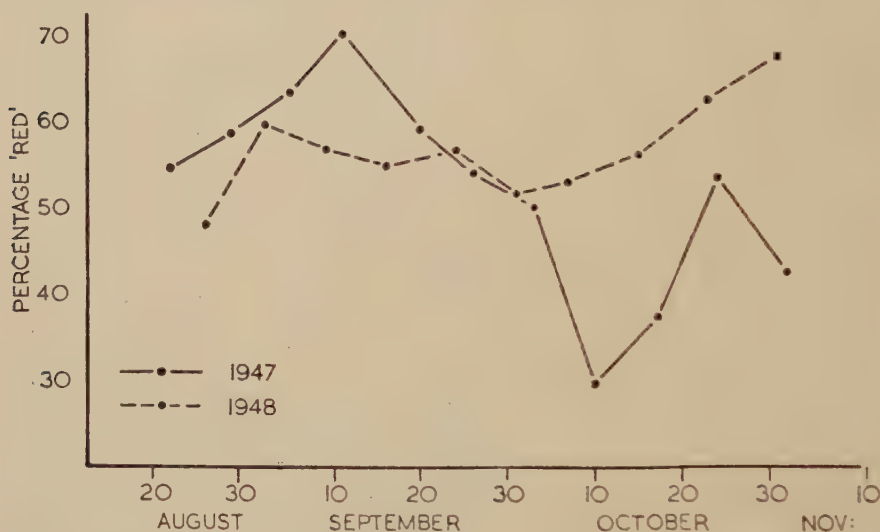


FIG. 5.

Laying and sucking of winter eggs of the Fruit Tree Red Spider Mite, *Metatetranychus ulmi* (Koch).

eggs are laid than are sucked by predators. The peaks correspond with the peak numbers of fourth and fifth generation adult females. In October there is a minimum percentage of red eggs, after which there is a steep rise.

It was not always possible to distinguish hatched summer eggs from sucked winter eggs, so that when summer eggs that were laid on the shoots hatched, the empty clear shells were included as "clear" eggs in the winter egg population counts. They were included in the total until the weather caused them to disintegrate or to fall off the shoot. This accounted for the bulk number of "clear" eggs in August and September. The rest of the "clear" eggs resulted from feeding of various predacious species, mainly *Anthocoris nemorum* (L.), *Orius majusculus* (Reuter), *Stethorus punctillum* (Weise), *Blepharidopterus angulatus* (Fallén) and *Conventizia pineticola* Enderlein (Collyer, 1949). The date of the minimum percentage of red

eggs in October corresponded with the date by which the Black-kneed Capsid *Blepharidopterus angulatus* (Fallén) individuals had all died and the *Anthocoris nemorum* (L.), *Orius majusculus* (Reuter) and *Stethorus punctillum* (Weise) adults went into hibernation. The last three species all hibernated at the same time and all the individuals did so within a few days. After this, the adult mites could normally lay winter eggs unhampered by predators, but in 1947 the orchard concerned had a high population of *Conwentzia pineticola* Enderlein, the larvae of which sucked many eggs. This does not show on the graph until the mites ceased laying in November, and then the percentage of "clear" eggs increased greatly until the predacious larvae spun up into cocoons in December, by which time there were barely 10 per cent. of the eggs still normal.

During the winter a few winter eggs were sucked, but from December to March there was normally only 10 to 15 per cent. reduction in numbers. Kuenen (1946) also notes this reduction during the winter, but records it as being 25 per cent.

(iii) *Effects of weather conditions.*

Favourable weather conditions will often cause a mite infestation to become far more severe than it would otherwise have been.

English and Turnipseed (1941) state that several phases in the life cycle of the allied mite *Paratetranychus citri* (McG.) are mathematically related to average temperature.

A spell of cold weather slowed down the metabolism of the mite and lengthened the instars. It will be noticed in Table VII that the immature life of mites of the first and second generations in spring and of the fifth generation in autumn was of longer duration than that of the third and fourth generations in the warmer months of July and August.

Weather also had an effect on the length of generations of the Fruit Tree Red Spider Mite as can be seen in Fig. 1, the first, second and fifth generations in the colder months of spring and autumn being longer. However, there would appear to be other factors influencing the length of a generation, because the second generation in 1949 was very long, summer eggs laid by the first generation not hatching until the first week of July. The generation was much longer than the equivalent one in 1948, although the temperature was consistently higher in June 1949, than in June 1948.

In the laboratory, the duration of the incubation period of the summer eggs appeared to be directly related to temperature. Table XI shows that in 1947 and 1949 the incubation period of summer eggs laid by the first generation in the cooler months of May and June was longer than that of the eggs of later generations of mites. The summer of 1948 was colder on the average than were those of 1947 or 1949 and Table XI also shows that the incubation periods of the eggs laid by the second and third generations in 1948 were longer than the corresponding periods in 1947 and 1949.

The figures for life-cycle, pre-oviposition period (Table VIII) and incubation period (Table XI) in the warm summers of 1947 and 1949 in this country agreed closely with those of Newcomer and Yothers (1929) for the Pacific Northwest, while in the cool summer of 1948 they approximated to those of Andersen (1948) for Germany.

During heavy rain all the mites were to be found on the under surface of the leaves huddled along the mid-rib and veins. They cling tenaciously with their claws and were not swept off by rain (see Table II). Kuenen (1946), however, gives figures that show a reduction in numbers after heavy rain. The mites also held on tightly to the leaves when a strong wind was blowing and were not easily dislodged.

TABLE II.

Mites and summer eggs of the Fruit Tree Red Spider Mite on 96 leaves from six trees before and after a very heavy thunderstorm.

		Eggs	Mites
Before rain (24.5.45)	..	129	344
After rain (27.5.45)	..	157	407

(iv) *Effect of spray programme.*

The introduction of Tar Oil as a winter wash for fruit trees was the primary cause of the mite becoming a major pest. This spray kills the eggs or hibernating adults of many of the insect predators of the mite and thus allows it to increase, unchecked, through its several generations in the summer. A further impetus was given to the mite population when DDT was applied as a summer spray. DDT is not toxic to the mites but destroys any predators which have escaped the winter Tar Oil. Further, it has such a long residual effect that any predators entering an orchard for some weeks after the application also succumb.

No summer spray has been found which is so effective against the mites that the population at the end of the season is less than that at the beginning. The sprays used kill off a larger or smaller percentage of the mites but they do not affect the eggs. The number of predators is also reduced by these sprays so that the mites hatching from the summer eggs are allowed to build up their population unchecked.

(v) *Dispersal phase of the mite.*

A large number of mites may be present in an orchard at the beginning of the season, the leaves bronze during the summer, and yet by the following autumn it may be difficult to find a winter egg (Garman & Townsend, 1938). It is here that the dispersal phase of the mite plays its part. The large population of mites reduces the food supply to such an extent that the adult females are forced to disperse to search for food material elsewhere. Thus a block of trees may have badly damaged foliage and yet it is almost impossible to find a single mite on the leaves, and very few winter eggs are laid. If a few of the dispersing mites chance to land in a clean orchard they will form a nucleus from which a large population can build up. Weather conditions play an important part at this point, as dispersal cannot take place unless they are suitable.

It has been shown that the majority of mites which disperse are adult females, but there are records of a few males and immature mites dispersing.

When the mite population in an orchard is large and the leaves are showing signs of damage, the mites often disperse. They do so by dropping on a silken thread (Steer, 1940) during a period of calm and then are caught up in a slight breeze and drift away. Stabler (1913) found mites 650 feet away from an infested orchard. The mites themselves are helpless once the thread is broken, so most of them probably perish before they reach a plant on which they can feed and so survive. The mites normally have only a few host plants and it seems likely that the authors' records of mites on some unexpected plants, e.g. weeds in the orchards, were due to the fact that the mites dispersed and happened to alight there. The few mites which reach a suitable host will soon multiply enormously, causing a severe infestation. The ability of the mite to disperse must be taken into account when field trials for the control of the pest are planned; for mites from unsprayed control trees soon spread on to the neighbouring trees where all the mites have been killed by sprays and may increase in numbers very quickly. Further, a hedge may be a source of infection to a clean orchard.

Work on dispersal is still in progress and a fuller account will be published later.

DESCRIPTION OF STAGES AND HABITS OF THE MITE.

The Fruit Tree Red Spider Mite overwinters as a winter egg on the fruit tree. In April and May the larva hatches and immediately starts to feed on the opening leaves. After a period of feeding, the larva passes into the quiescent stage from

TABLE III.

Proportion of mites and summer eggs of the Fruit Tree Red Spider Mite on the lower and upper leaf surfaces.

	Mites				Summer eggs			
	Lower		Upper		Lower		Upper	
	No.	%	No.	%	No.	%	No.	%
1945	65,056	82	14,469	18	29,064	85	5,193	15
1946	75,315	74	26,205	26	43,585	80	10,706	20
1947	150,230	75	50,004	25	88,202	74	31,611	26
1948	12,037	80	3,040	20	12,356	80	3,011	20
1949	66,048	70	27,785	30	80,315	72	31,954	28

which it emerges as a protonymph. The protonymph feeds and passes into the second quiescent stage and emerges as a deutonymph which in turn becomes an adult male or female after a third quiescent stage. Some males pass through only one nymphal stage.

Unless they are very crowded, the mites feed on the under surface of the leaves and, when feeding, they are generally alongside the veins. The numbers of mites and summer eggs on the lower and upper surfaces of leaves recorded by the imprint method are shown in Table III. These figures are the totals of mites and summer eggs recorded on 80 leaves every third day in each season, giving a total of between 3,000 and 4,000 leaves per year. As the weather conditions varied from day to

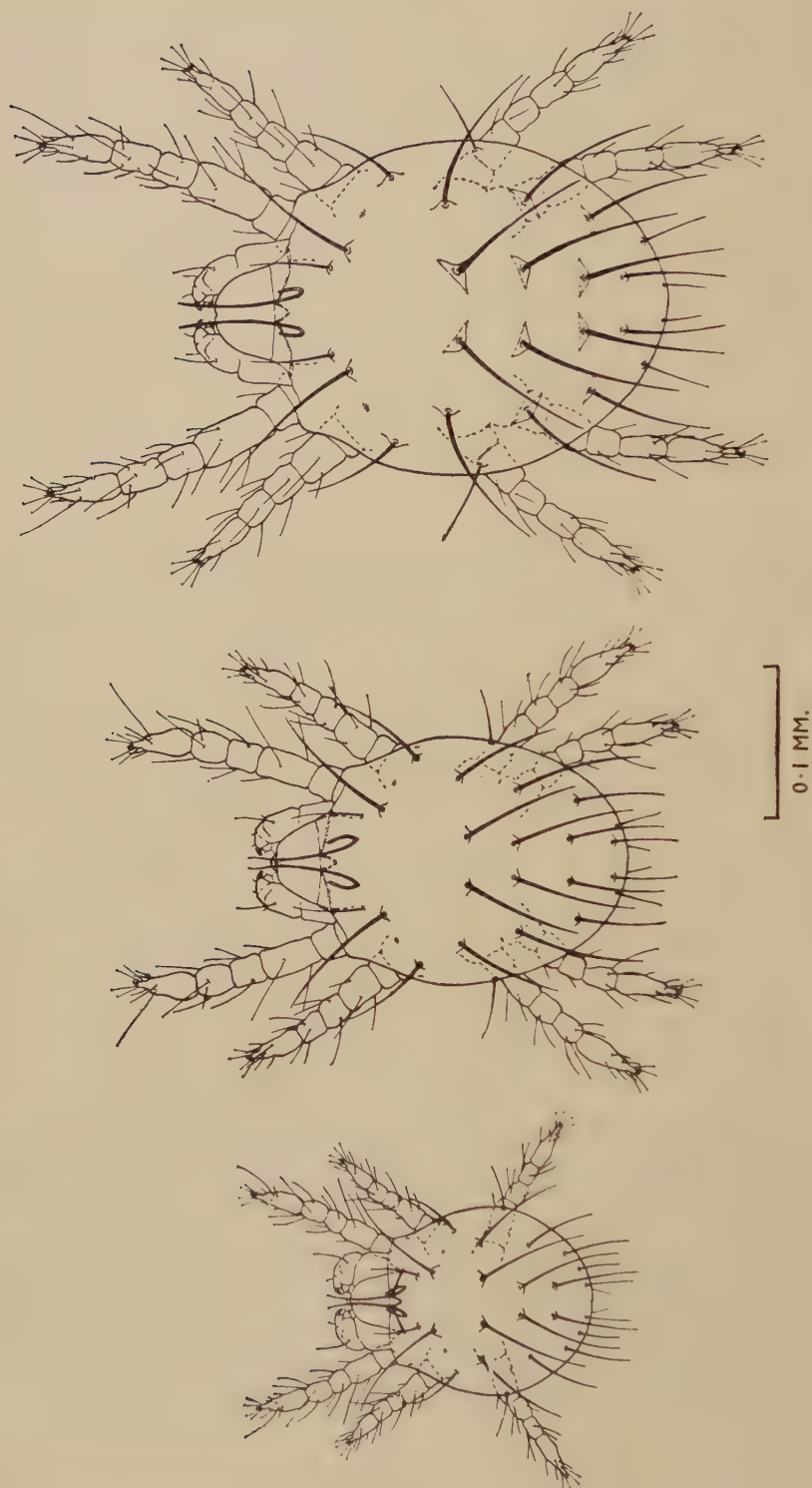


FIG. 6.

Fruit Tree Red Spider Mite, *Metatetranychus ulmi* (Koch), larva, protonymph and deutonymph. Dorsal view, drawn from mounted specimens ($\times 200$).

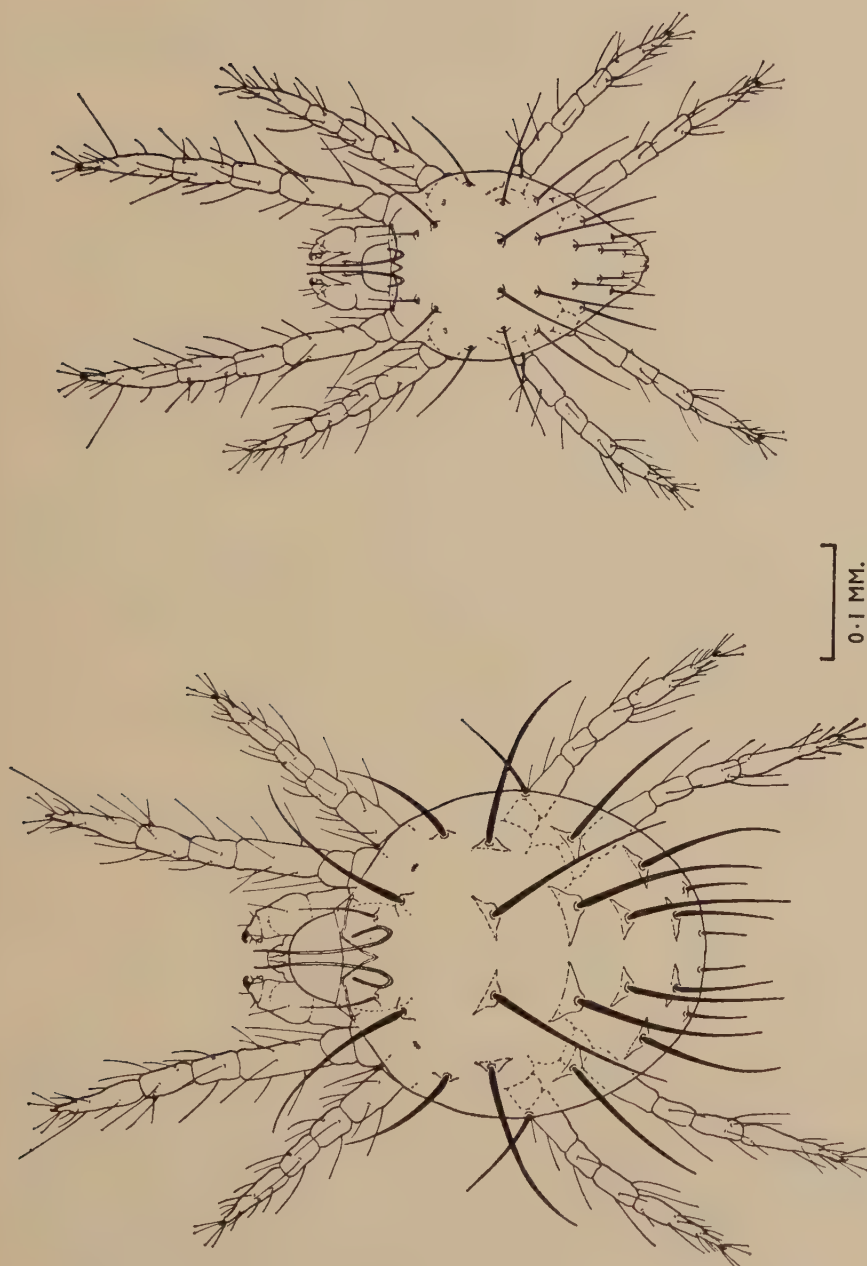


FIG. 7.

Fruit Tree Red Spider Mite, *Metatetranychus ulmi* (Koch), adult female and male. Dorsal view, drawn from mounted specimens ($\times 150$).

day throughout each season, the final totals in each year give an idea of the percentage of mites and eggs on the upper and lower leaf surfaces on an average day in that year.

During bright sunny periods the adult female mites are found on the upper surface of the leaves, but if cloudy conditions occur they quickly retire to the lower surface.

Winter eggs and summer eggs.

The winter eggs are "onion-shaped", slightly flattened on top, the outer waxy coat being prolonged into a conspicuous spine on top. The spine is hooked at its extremity and, immediately the female has laid the egg, she produces three or four silken "guy ropes", attaches them to the hook and anchors the egg to the twig. The winter eggs are bright red and are laid on the smaller branches and twigs. Most are laid on the under side (Günthart, 1945), and concentrated round the buds and between the first- and second-year wood. If the mite population builds up in autumn, winter eggs may also be laid on the larger branches and the trunk, giving the whole tree a distinctly red appearance. Very occasionally, winter eggs are laid on the leaves and fruit.

The summer eggs are very similar to the winter eggs but are slightly smaller (Table IV) and paler. When laid they may be yellow or pale green, but soon deepen to orange. The female anchors the summer eggs also by "guy ropes". Most of the summer eggs are on the lower surface of the leaf (Table III). Later in the year a few summer eggs are laid on the shoots.

TABLE IV.

Diameter of eggs of the Fruit Tree Red Spider Mite (in mm.).

			Maximum	Minimum	Average
Winter	..	..	·16	·14	·15
Summer	..	..	·15	·13	·14

This difference is significant at a level of $P < 0.001$.

When the egg is about to hatch, the shell splits around the equator but the two halves are not completely severed. The top portion opens as if on a hinge. The mite emerges by forcing the lid open by means of the spines on its dorsum. The front legs protrude and hang over the side of the shell, the mite crawls out, and the lid usually springs back to its original position. The time required for the mite to emerge is approximately $3\frac{1}{2}$ minutes. The mites are active from the moment of emergence and when the first generation larvae emerge from the winter eggs they invariably move upwards and start to feed on the leaves.

The various stages of the mite, drawn from slides, are shown in Figs. 6 and 7; average sizes are given in Table V.

Larva.

The larva is easily distinguished from all the other stages as it has only three pairs of legs. On emerging from the winter egg it is pale orange but, after feeding, soon darkens to red. The larvae hatching from the summer eggs vary very much in colour, ranging from the pale yellow through orange to a bright green. On the dorsal surface of the mite are 26 pilose setae, which are present in all the stages.

TABLE V.

Body length of various stages of the Fruit Tree Red Spider Mite (in mm.).

	Maximum	Minimum	Average for 12
Larva	·20	·15	·17
Protonymph	·25	·20	·23
Deutonymph	·30	·25	·27
Adult female	·40	·30	·36
Adult male	·33	·25	·26

After feeding for a time, the larva settles down on the under surface of the leaf and passes into the quiescent stage, which usually lasts as long as the previous feeding period. It remains motionless and always assumes the same attitude with its forelegs curved round the palpi. As the old skin loosens from the new one it becomes white and shiny, and soon a transverse split occurs across the dorsum between the second and third pairs of legs. As the mite begins to move, the split widens and the mite emerges, pulling out the forelegs first, which can then grip the leaf and allow the back legs to be withdrawn. The moult skins remain attached to the leaves as do the empty shells of the hatched summer eggs. A similar quiescence occurs between the stages following.

Protonymph.

The protonymph has four pairs of legs and is larger and of a darker colour than the larva.

Deutonymph.

The deutonymph and protonymph are very similar, but they can be distinguished by the number and arrangement of the setae on the ventral surface (Fig. 8). During this stage the sexes can often be distinguished, the deutonymph which is to become a male being more slender.

Adult female.

The female is round, robust and has a decidedly curved back. On emerging from the moult skin her colour is a bright, clear red but with age she darkens to very deep red. The tubercles of the 26 dorsal bristles show up as distinct white spots against her general colour. The genital opening can be seen when the mite has moulted from a deutonymph to an adult female. The structure of the palpi, the tarsi and the trachea is described and figured by Geijskes (1939).

The females of the Fruit Tree Red Spider Mite spin a small amount of webbing, but it is only when the populations are very high that it becomes conspicuous.

The webbing will be found on the leaves between the blade and the petiole and covering the winter eggs on the twigs. During the autumn of 1949 several orchards in Essex had very large populations of mites and the trees were clothed with webbing. It festooned the twigs and covered the buds and was very apparent in the angles between the twigs and the branches where it entangled a writhing mass of mites. In very bad cases the webbing extended down and around the trunks.

Adult male.

The male is smaller than the female and more slender. Because of its smaller size, the legs of the male appear to be longer than those of the female, but are approximately the same length. The colour is pale orange on emergence, turning to dark orange with feeding. The structure of the penis is figured by Geijskes (1939).

Copulation.

The male passes through the feeding and quiescent stages in a slightly shorter time than does the female and is running over the leaves while the female is still a quiescent deutonymph. The male chooses a quiescent deutonymph and remains beside her until the female emerges when copulation immediately takes place. Newcomer and Yothers (1929) state that the male assists the female in her emergence from the moult skin but this has not been verified during the authors' observations. The female after her first fertilization is not again approached by a male, but a male can fertilize more than one female.

Number of nymphal stages in male life history.

In 1938 Geijskes recorded that the male of the Fruit Tree Red Spider Mite had only one nymphal stage while the female had two. However, from the authors' records, it appeared that the male can have either one or two nymphal stages. Both developed in the brood of eggs from a single female, and both occurred in the offspring of fertilized and parthenogenetic females. No explanation can be given of this phenomenon but it is suggested that it may be a character inherited through the female.

Development of ventral setae.

In addition to the 26 pilose dorsal setae, the mites have a number of simple ventral setae. Geijskes (1939) figures the ventral surface of an adult female of *Schizotetranychus schizopus* (Zacher) showing these setae and in *Metatetranychus ulmi* (Koch) the arrangement is the same. The immature stages have fewer ventral setae than have the adult females, and the authors have found that the stages can be identified by the number and position of these setae. Fig. 8 is a diagrammatic representation of this development. The adult male and female have the same number of setae, and those by the palpi and coxae are similarly placed. The seta No. 11 is more posteriorly placed in the male than in the female. Seta No. 16, is on the ventral surface of the female but on the dorsal surface of the male; however, it cannot be mistaken for a true dorsal seta as it is not pilose.

The larva has only seven ventral setae; the protonymph has twelve and the deutonymph has sixteen (Fig. 8). When the mite becomes adult only one more is added and this is situated by the genital organ.



FIG. 8.

Fruit Tree Red Spider Mite, *Metatetranychus ulmi* (Koch), developmental changes in chaetotaxy. L = Larva; P = Protonymph; D = Deutonymph; and the female and male adult mites. In the immature stages, only the additional setae are numbered; in the adults the underlined seta, No. 12, is the only addition.

Immature mites of both sexes have the same number of ventral setae. Mites which had only one nymphal stage before developing into males have the same arrangement of ventral setae as have those which had two nymphal stages and males resulting from fertilized and non-fertilized eggs have the same number of ventral setae.

FIELD AND LABORATORY OBSERVATIONS.

Hatching of winter eggs.

Table I shows that hatching of winter eggs of the Fruit Tree Red Spider Mite occurred in Essex during the last week of April.

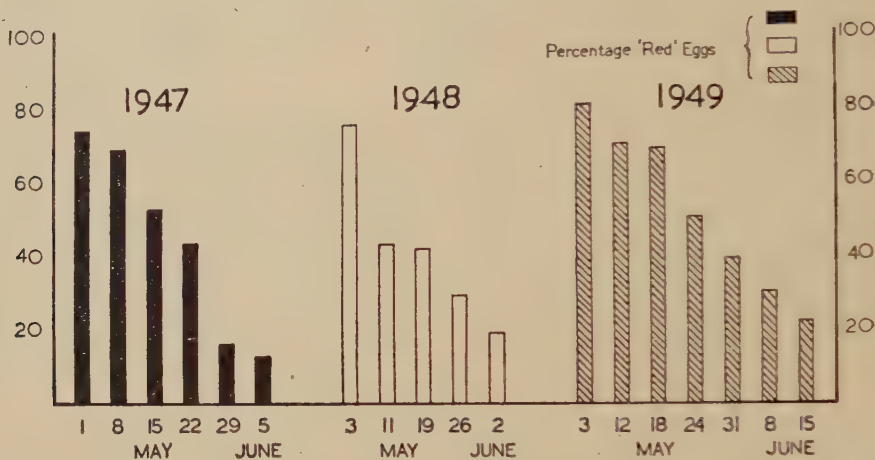


FIG. 9.

Hatching of winter eggs of the Fruit Tree Red Spider Mite, *Metatetranychus ulmi* (Koch).

Newcomer and Yothers (1929) state that hatch takes place in the middle of April in the Pacific Northwest, Kuenen (1942) gives the 19th May for Holland and Andersen (1948) the middle to the end of April for Germany.

The main hatching of winter eggs did not occur until three weeks later, and varied from year to year and from orchard to orchard in any season, depending directly on the date of first hatch.

In 1947, hatching of winter eggs was completed by 2nd June and, in 1949, by 13th June but, in 1948, hatching was still taking place on 25th June. These late dates of hatch were isolated cases, the main hatch taking place earlier, but it meant that in 1948 the first and second generations overlapped.

When an egg hatches or has its contents sucked out by a predator, only the egg shell remains and it appears white and glassy in comparison with the red unhatched egg. Such eggs are described as "clear".

In the histogram (Fig. 9) the eggs are not 100 per cent. red before hatching commences, because of the activities of predaceous insects and mites during the autumn and winter. It was impossible to distinguish with certainty between "clear" eggs due to the sucking of insects and "clear" eggs due to the hatching of mites. In the diagram the column representing red eggs includes all those which

were not "clear". This number was made up of those which were apparently normal and those which showed a clear dividing line down the centre of the egg, the contents having drawn into one half, the other half being clear. These eggs were dead and would remain on the trees until weathered away. The small percentage of red eggs left when hatching was complete consisted of these infertile eggs which would eventually disappear.

Factors affecting the hatching of winter eggs.

The factors influencing the time of the first hatching of the winter eggs of the Fruit Tree Red Spider Mite in a commercial orchard are, (1) the previous spraying programme, (2) situation of the orchard and (3) the weather conditions prevailing in April and early May. It is very difficult to disentangle these factors and to assign to one of them the chief role in bringing about the first hatch of the season in an orchard.

As a result of daily observations in a number of orchards and compilation of a table such as Table VI it appears that the main factor influencing time of hatch is the previous spraying programme, but there is also the secondary factor of the situation of the orchard.

The first hatch was always observed in a derelict orchard, centre G, which received no spray of any kind. This observation agrees with that of Kuenen (1942).

Table VI shows that first hatch in a commercial orchard in 1947 took place on trees which had had no winter spray, followed by hatch on those sprayed with tar oil, DNC, Thiol, and petroleum respectively. The late hatch on Worcester Pearmain trees sprayed with tar oil at centre A, on the 9th May, was probably because this farm lies in an exposed position and at an altitude approximately 50 feet higher than the other centres visited. It will be noted that the late hatch on Bramley's Seedling sprayed with DNC also occurred at centre A.

Observations in the other seasons confirmed these findings. Hatching occurred at centre A in 1948 on 27th April, six days later than at another centre (X), where first hatch was on 21st April. This orchard, although only $2\frac{1}{2}$ miles distant from centre A, is in a sheltered position and at an altitude approximately 100 feet lower. In 1949, hatch at centre X was on the 21st April and at centre A on the 2nd May. Both orchards had the same winter spray treatment.

In one season, observations were made on trees in several orchards to ascertain if there was any correlation between the first hatching of winter eggs and the north, south, east or west side of the tree. No evidence was obtained of any such correlation.

In 1947, after a very severe winter, the first larvae were not seen until 30th April, while in the other seasons, after much milder winters, larvae were seen a week earlier (21st April).

Hatching in the laboratory.

If twigs bearing winter eggs are brought into the laboratory and are kept in pots of damp sand, these eggs will hatch earlier than the eggs in the field. Those brought into the laboratory just after the diapause has ended, will hatch earlier than those brought in at an earlier date. Eggs brought in on 8th March hatched on 24th April, while those brought in on 24th March hatched sixteen days earlier, on the 8th April.

In December, prunings of Worcester Pearmain and Cox's Orange Pippin covered with winter eggs were brought into the laboratory and several pieces were left on a bench until April. It was then noticed that hatch of the winter eggs was taking place. The twigs were quite dead, having had no water for over four months.

TABLE VI.

Dates of the first hatching of winter eggs of the Fruit Tree Red Spider Mite in a number of orchards.

Date	Variety	Winter spray	Centre
21st April	Unknown	None	G
30th April	Laxton's Superb	None	A
2nd May	Laxton's Superb	None	D
3rd May	Laxton's Superb	Tar oil	C
	Beauty of Bath	Tar oil	E
5th May	Bramley's Seedling	Tar oil	D
	Worcester Pearmain	Tar oil	D
	Beauty of Bath	Thiol	D
6th May	Cox's Orange Pippin	Tar oil	C
	James Grieve	Tar oil	C
	Cox's Orange Pippin	DNC	E
	James Grieve	DNC	E
	Worcester Pearmain	DNC	E
	Laxton's Superb	DNC	E
	Worcester Pearmain	Tar oil	F
7th May	Monarch	Tar oil	D
	Cox's Orange Pippin	Thiol	D
	James Grieve	Thiol	D
8th May	James Grieve	Petroleum	B
	Laxton's Superb	Petroleum	B
9th May	Worcester Pearmain	Tar oil	A
10th May	Ellison's Orange	Petroleum	B
	Worcester Pearmain	Petroleum	B
	Cox's Orange Pippin	Petroleum	B
13th May	Bramley's Seedling	DNC	A
	Early Victoria	Petroleum	B

Breeding of mites in the laboratory.

In the past, one of the chief difficulties encountered by workers on the biology of the Fruit Tree Red Spider Mite was to devise a successful method of rearing mites so that they could be examined daily. Newcomer and Yothers (1929) used rearing cells made of felt and celluloid fixed to leaves of small trees by paper clips. In this country such cells have not proved very satisfactory and a new method had to be devised by the writers. A thin layer of fine sand was put into a petri dish and covered with filter paper. Three leaves of suitable size were placed

in the dish; if they did not fit very well, the petioles were cut. The filter paper under each leaf was marked to distinguish between them. The sand and filter paper were kept sufficiently moist to prevent the leaves wilting and the mites roaming from the leaves. The amount of moisture had to be carefully regulated. The mites tended to roam from the leaves more readily when adult than when in the immature stages, so it was then essential to keep the conditions correct. At all times the inner surface of the lid of the petri dish had to be kept dry.

One mite was kept on each leaf and its development recorded daily. Note was made of quiescent stages and the occurrence of ecdysis.

TABLE VII.

Total immature life of female and male Fruit Tree Red Spider Mites (in days).

	1st gen.	2nd gen.	3rd gen.	4th gen.	5th gen.
<i>Females</i>					
1947	11.7 (16)	11.7 (21)	8.8 (91)	8.9 (76)	11.9 (49)
1948	15.2 (11)	14.6 (21)	12.2 (6)	13.7 (7)	—
1949	12.8 (15)	10.2 (17)	8.8 (15)	9.0 (9)	17.0 (2)
<i>Males (2 nymphal stages)</i>					
1947	8.2 (4)	12.2 (4)	8.0 (3)	9.5 (2)	12.0 (2)
1948	15.0 (6)	12.8 (16)	12.6 (7)	10.7 (4)	—
1949	12.5 (6)	8.6 (13)	7.5 (6)	8.0 (3)	7.0 (1)
<i>Males (1 nymphal stage)</i>					
1947	9.6 (9)	9.3 (14)	7.5 (42)	7.6 (45)	9.8 (36)
1948	13.2 (5)	12.0 (11)	10.7 (6)	10.0 (2)	—
1949	—	8.7 (7)	7.0 (2)	7.0 (2)	—

The mean of n observations has a standard error, $\frac{2.4}{\sqrt{n}}$ for females, and $\frac{1.8}{\sqrt{n}}$ for males. The number in brackets is the number of observations made.

When an adult female matured, a male was introduced on to the leaf, unless she was to be used for parthenogenetic studies. At the commencement of egg-laying a plan of the leaf was drawn; the eggs were marked on the plan as they were laid and their times of hatching were recorded.

As the fifth generation females laid winter eggs on the wood it was necessary to offer them an alternative oviposition site. A piece of twig in the petri dish with the leaf was used the first season, but this was not satisfactory. Massee (1947) described a new method of rearing mites on apple seedlings. One of these seedlings which was free from mites, had all but one of its terminal leaves removed and was then cut at a suitable height. The twig was placed in a flower pot of sand enclosed in a hurricane lamp glass, the top of which was covered with muslin. The mite thus had both leaf and twig on which to live. It was only necessary to use this method for adult females of the fifth generation.

Results of experimental rearing of mites in the laboratory.

Table VII shows the total number of days of the immature life of female and male mites. In nearly every instance, individuals of the third and fourth generations took significantly less time to mature than did individuals of the first, second

or fifth generations. The figures for 1948 were significantly lower than for 1947 and 1949 for all generations of females and for all but second and fourth generations of males with two nymphal stages and for fourth generation males with one nymphal stage.

Combining all the data, males with two nymphal stages took significantly longer to mature than did those with only one nymphal stage.

Never was the immature life of a male significantly greater than the immature life of a female, but sometimes the immature life of a female was significantly greater than the immature life of the male.

TABLE VIII.

Average time from emergence to last oviposition of females of the Fruit Tree Red Spider Mite (in days).

Generation			Pre-oviposition period			Oviposition period			Total		
			1947.	1948.	1949.	1947.	1948.	1949.	1947.	1948.	1949.
1st	..	..	2.9	4.1	2.5	9.2	14.0	12.6	12.1 (11)	17.8 (17)	15.1 (13)
2nd	..	..	3.4	3.9	2.7	10.0	12.6	9.7	13.7 (18)	16.5 (22)	12.5 (15)
3rd	..	..	2.6	2.8	3.8	8.5	18.0	8.1	11.4 (25)	20.7 (4)	11.9 (12)
4th	..	..	2.9	—	3.7	9.2	—	6.0	12.3 (24)	—	9.7 (3)

The mean of n observations has a standard error $\frac{7.9}{\sqrt{n}}$. The number in brackets indicates the number of observations made.

The average time elapsing before an adult female laid eggs and the average oviposition period are shown in Table VIII. This Table includes only those females which laid eggs. The figures in Table VIII do not show any significant differences except for the third generation, when the pre-oviposition and oviposition periods were longer in 1948 than in 1947 or 1949. The pre-oviposition period varied from less than a day up to seven days and the oviposition period from one to thirty-three days.

TABLE IX.

Average length of adult life and number of eggs laid by females of the Fruit Tree Red Spider Mite.

Generation	Total adult life (days).			No. of eggs laid.		
	1947.	1948.	1949.	1947.	1948.	1949.
1st ..	9.3 (17)	14.8 (25)	15.6 (17)	6.5 (17)	12.6 (25)	15.8 (17)
2nd ..	13.6 (21)	14.8 (28)	12.2 (17)	13.4 (21)	8.7 (28)	12.4 (17)
3rd ..	11.1 (30)	17.4 (5)	11.2 (15)	14.5 (30)	14.2 (5)	9.9 (15)
4th ..	12.2 (28)	25.2 (5)	9.6 (5)	10.1 (28)	—	7.0 (5)
5th ..	—	—	27.2 (6)	—	13.1 (10)	13.2 (8)

The mean of n observations has a standard error $\frac{7.8}{\sqrt{n}}$ for length of life and $\frac{10.4}{\sqrt{n}}$ for number of eggs laid. The number in brackets is the number of observations made.

Table IX includes all females, the life of which was recorded, whether they laid eggs or not, giving the total adult life from emergence to death, which includes a period of up to six days after the last egg had been laid.

Figs. 10 and 11 show in histogram form the life span of females of several generations and the number of eggs laid by individual mites. Every recorded female in each generation is included. These figures, obtained in the laboratory, are substantiated by field records.

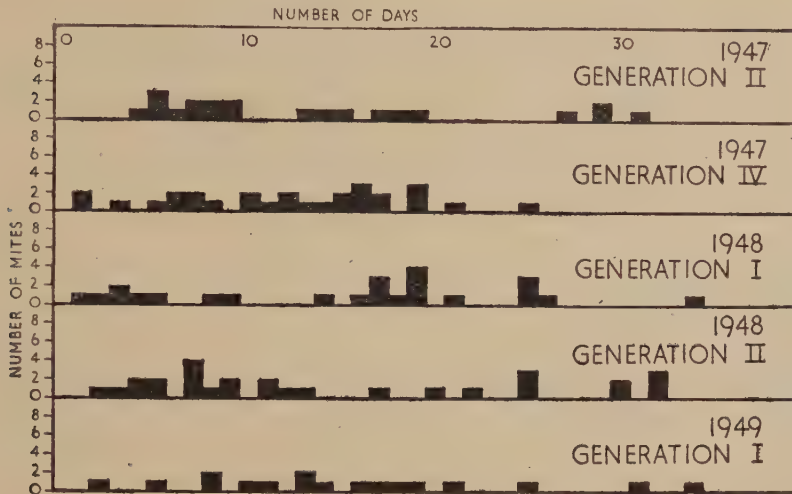


FIG. 10.

Length of adult life of females of the Fruit Tree Red Spider Mite, *Metatetranychus ulmi* (Koch).

In 1947 a successful technique had not been found for breeding fifth generation mites and obtaining winter eggs, so no results are given. In 1948 the fourth generation females did not lay summer eggs in the laboratory, although they did in the field. Therefore, the females of the fifth generation used in the laboratory were new individuals of which the ancestry was not known. Apart from this instance, the mites used were all descended from the individuals with which the colony was started at the beginning of the season.

For two weeks in August, 1949, the summer eggs laid were recorded twice daily, at 9.30 a.m. and 4.30 p.m. (B.S.T.); 48 per cent. were deposited between 4.30 p.m. and 9.30 a.m. and 52 per cent. between 9.30 a.m. and 4.30 p.m. The tendency was for two eggs to be deposited every 24 hours at almost regular intervals.

There were no significant differences in the numbers of eggs laid, except for the first generation in 1947, which gave a significantly smaller number than that laid by the second and third generations. The fifth generation females in 1949 had a significantly longer adult life than had females of the other generations.

The average length of adult life of the males is shown in Table X. The males were very active and, under artificial conditions, it was difficult to keep them on a leaf for a normal lifetime. Therefore, the average given may be a little shorter than it would have been in the field.

TABLE X.

Average adult life of males of the Fruit Tree Red Spider Mite (in days).

Generation	1947.	1948.	1949.
1st ..	7.1 (10)	6.7 (7)	10.0 (5)
2nd ..	9.0 (4)	6.3 (9)	9.8 (19)
3rd ..	8.4 (9)	6.2 (4)	7.7 (6)
4th ..	7.8 (13)	6.4 (5)	7.7 (4)
5th ..	6.9 (7)	—	—

The mean of n observations has standard error $\frac{2.8}{\sqrt{n}}$. The number in brackets indicates the number of observations made.

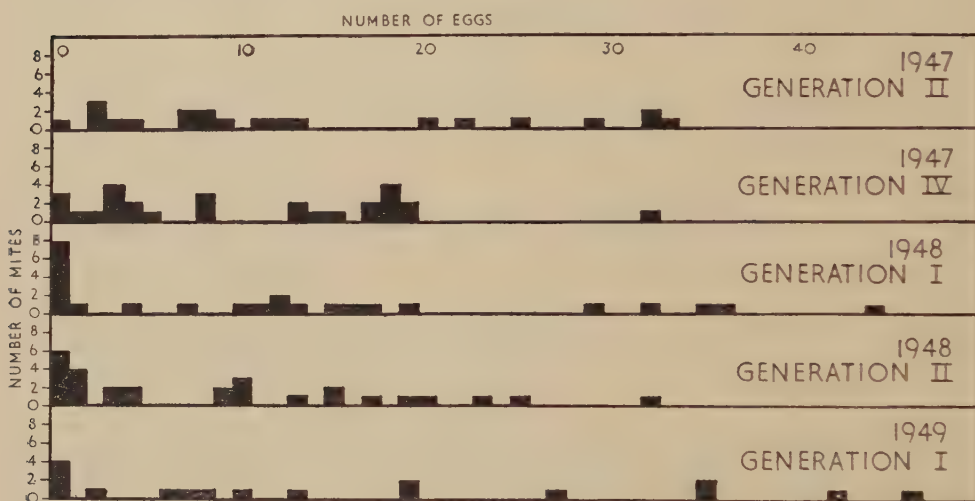


FIG. 11.

Number of eggs laid by adult females of the Fruit Tree Red Spider Mite, *Metatetranychus ulmi* (Koch).

TABLE XI.

Average incubation period of summer eggs of the Fruit Tree Red Spider Mite (in days).

	1947.	1948.	1949.
Laid by 1st generation ..	12.1 (56)	13.9 (217)	10.7 (182)
Laid by 2nd generation ..	10.2 (167)	16.2 (119)	8.7 (138)
Laid by 3rd generation ..	8.2 (277)	11.6 (39)	8.8 (72)
Laid by 4th generation ..	8.9 (175)	—	8.7 (20)

The mean of n observations has a standard error $\frac{3.0}{\sqrt{n}}$. The number in brackets is the number of observations made.

Adult females lived longer than did adult males in every generation in each year, and the difference was significant in half the instances.

The average incubation period of summer eggs is given in Table XI. The minimum recorded was three days and the maximum 25 days. The incubation period was always significantly shorter for the third and fourth generations than for the first and, in 1947 and 1948, than for the second generation also. In 1948 the incubation period was always significantly longer than in 1947 and 1949.

Summary of life history. There was an average incubation period of 11 days, a larval period of four days, a nymphal period of eight days and a pre-oviposition period of three days, giving a complete life cycle of 26 days.

The females oviposited for approximately 11 days and laid an average of 1.1 eggs a day giving a total of approximately 12 eggs per female. The actual average was 11.2 eggs. One female, however, laid 46 eggs.

The females lived an average of 12 days and the males 10.5 days. The longest time a female lived was 34 days and a male 22 days.

Sex ratio.

If all adult female mites were fertilized and produced normal eggs it would be expected that a population would arise in which the sex ratio was 1 male : 1 female. Parthenogenesis, resulting in only males being produced, should cause the ratio to favour the males. Research workers, however, have always given sex ratio figures which favour the females, Ross and Robinson (1922) 1 male : 10 females and Newcomer and Yothers (1929) 2 males : 3 females.

Sex ratio counts of populations in the field were done at various times throughout 1948 and 1949, an attempt being made each time to include only mites from a single generation. The figures obtained varied from 1 male : 2 females to 1 male : 6 females. It must be remembered that the males mature more quickly than the females, so that if the counts are made at the wrong time a false impression may be obtained. It is clear, however, that the proportion is always in favour of the females though the actual ratio may be greatly affected by the conditions in different orchards.

Parthenogenesis.

A special study of parthenogenesis in the Fruit Tree Red Spider Mite was made and the results are set out in Table XII. Every female mite left unfertilized in the laboratory breeding experiments laid eggs, and from these eggs only males were produced. Fertilized females laid eggs from which males and females were produced.

Several workers, including Ross and Robinson (1922), Hamilton (1924) and Newcomer and Yothers (1929), have stated that the female of the Fruit Tree Red Spider Mite can reproduce parthenogenetically.

Table XII shows that parthenogenesis had no significant effect on any part of the life history of the mite. The difference in means was not significant except for the incubation period in 1949. This was significantly greater for unfertilized eggs than for fertilized ones. There was no significant difference between the incubation periods in 1948, so too much attention need not be given to the small difference in 1949.

TABLE XII.

Results of a study of parthenogenesis in the Fruit Tree Red Spider Mite.

	1948.			1949.		
	Fertilized.	Un-fertilized.	Significant difference (P=0.05).	Fertilized.	Un-fertilized.	Significant difference (P=0.05).
Life of female (days)	16.7	14.6	5.0	12.0	12.5	3.8
Life of male (days)	—	—	—	11.1	8.4	4.2
Number of summer eggs laid by female	15.0	13.7	6.5	13.1	17.6	6.2
Percentage hatch of summer eggs ..	48.2	43.1	23.8	69.5	66.8	15.1
Incubation period of summer eggs (days)	14.3	14.6	0.9	9.1	10.0	0.4
Number of summer eggs per day ..	1.2	1.1	0.3	1.8	1.5	0.5
Pre-oviposition period of female (days)	3.8	3.9	1.2	3.3	2.8	1.0

HOSTS AND DAMAGE.

Hosts.

The records in the literature of the host plants of the Fruit Tree Red Spider Mite are very numerous. In all, there are records of its occurrence on more than 80 species of plant, over half of which are included in the family Rosaceae (Mabry and Walton, 1939; Newcomer and Yothers, 1929; and Listo *et. al.*, 1939).

In this country *Metatetranychus ulmi* (Koch) is chiefly a pest of apple but bad infestations have been seen by the authors on plum, greengage, damson and pear. Winter eggs and summer stages have also been found on many cultivated and hedgerow plants including raspberry, cherry, elm (*Ulmus* sp.), hawthorn (*Crataegus oxyacantha* L.), sloe (*Prunus spinosa* L.)—the large-leaved variety *P. insititia* being most heavily attacked—poplar (*Populus* sp.), willow (*Salix* sp.), Myrobalan plum (*Prunus cerasifera* Ehrh.), dog rose (*Rosa canina* L.), crab apple (*Prunus malus* L.), flowering currant (*Ribes sanguineum* Pursh.), and *Cotoneaster* sp.

The authors have also found that the mite can establish itself on various weeds when these are growing below trees carrying a large population of mites. These weeds are: common bryony (*Bryonia dioica* Jacq.), black bindweed (*Polygonum convolvulus* L.), bindweed (*Convolvulus arvensis* L.), common stork's bill (*Erodium cicutarium* L'Her.), groundsel (*Senecio vulgaris* L.), broad dock (*Rumex obtusifolius* L.), common mallow (*Malva sylvestris* L.), germander speedwell (*Veronica chamaedrys* L.), corn gromwell (*Lithospermum arvense* L.), fat hen (*Chenopodium album* L.) and buttercup (*Ranunculus* sp.).

Varietal Resistance. Massee (1929) names five varieties of apple (Lord Derby, Allington Pippin, Worcester Pearmain, Laxton's Superb and Orleans Reinette), which are severely attacked by *Metatetranychus ulmi* (Koch). The writers have studied the habits of the mite on many apple varieties, including Cox's Orange Pippin, Worcester Pearmain, Laxton's Superb, James Grieve, Miller's Seedling,

Beauty of Bath, and Bramley's Seedling. All these varieties were observed with severe infestations and only the last variety seemed to be at all resistant. The leaves of Bramley's Seedling were often bronzed and damaged but, even when severely attacked, defoliation was never seen, whereas it was observed on all the other varieties. Garman (1923) states that the thin-leaved varieties of apple are most susceptible to damage and Lewis (1945) lists the varieties and the severity of attack. He states that resistance to attack is an inherited character and that the triploid varieties are less susceptible. Of those listed above, the only triploid variety is Bramley's Seedling.

In stone fruits, the authors have found that the plum variety Victoria is not often badly attacked and, even when an infestation does occur, very little damage is done. The other varieties of plum and damson are often badly attacked especially Farleigh and Merryweather damsons and Czar, Yellow Egg and Giant Prune plums.

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Reduction of fruit size on badly infested trees is recorded by Listo, Listo and Kanervo (1939), Frost (1919), Garman (1923) and Hey (1944). Ross and Robinson (1922) also record loss of fruit size and weight and also note a check to wood growth. Cory (1923) records a reduction in the size of fruit buds.

Small and badly coloured fruits have frequently been noticed by the writers on infested trees and figures will be published later that show a definite difference in fruit size and colour between sprayed and unsprayed trees.

The Fruit Tree Red Spider Mite feeds usually on the under-surface of the leaf by inserting its fine needle-like stylets through the epidermis and withdrawing the plant juices. One mite feeding on a leaf for only half an hour produces internal leaf damage and thus reduces the efficiency of the leaf. Much internal damage is caused by the feeding of the mites before any sign of external damage is evident.

The mouthparts of the allied mite *Tetranychus telarius* (L.) are described and figured by Blauvelt (1945). They consist of a ventral portion, the rostrum, with a median U-shaped groove in which moves the dorsal mandibular plate. The basal portions of the stylets are embedded in the mandibular plate. The plate is extended and contracted by powerful muscles. In puncturing the leaf tissue during feeding, the stylets are activated by a rapid "in and out" movement of the mandibular plate as well as by muscles attached to the stylets. This rapid "in and out" movement has often been noted when the authors were observing the mites feeding.

The literature contains very many references to the characteristic external appearance of infested apple and plum leaves, and Trägårdh (1915) and Geijskes (1938) figure cross-sections of leaves to illustrate the internal damage caused to the leaves by mite feeding.

External damage to the leaves, on which a large and increasing population of mites are feeding, is shown in a distinct series of stages. At first the leaf shows a faint white speckling; then, as the number of feeding punctures increases, the areas of damage spread and the whole leaf assumes a dull greyish green colour.

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External damage to the leaves, on which a large and increasing population of mites are feeding, is shown in a distinct series of stages. At first the leaf shows a faint white speckling; then, as the number of feeding punctures increases, the areas of damage spread and the whole leaf assumes a dull greyish green colour.

In bad attacks the leaf is bronzed, while, in the final stage, which only occurs when the leaf has had a very severe attack, it becomes a silvery grey.

Leaves were sectioned by the writers at the various stages of external damage and it was found that the mite forced its stylets through the lower epidermis and spongy mesophyll layer and penetrated a cell of the palisade mesophyll layer. The damaged cell shrank in size and the contents appeared to coagulate and retreat into the end of the cell (Fig. 12). In very badly damaged cells there was evidence that the complete contents of the palisade cells were removed. Cells of the spongy mesophyll were damaged, but only occasionally, as they were relatively few in number and widely scattered. No attempt was made by the mite to penetrate the vascular bundle. In comparing sections of damaged and undamaged leaves (see Fig. 12) it was very noticeable that the damaged leaves showed many flattened epidermal cells especially on the lower surfaces. Apparently these were destroyed by the mite in its attempt to reach the underlying tissue.

Only the cell which was actually penetrated by the stylets was damaged. The damage did not spread to adjacent cells.

The disappearance of chlorophyll and drying-out of the cells considerably reduces the water content of the leaves and this is further aggravated if the season is a very dry one. Thus, in a year of drought, mite damage occurs early in May and June, is very severe in degree and leaf drop may occur in August (Wiesmann, 1940). Under more normal conditions, severe bronzing of foliage does not occur until late July or August and the trees do not drop their leaves prematurely.

These observations suggest an explanation of the fact that two varieties of apple can have a similar infestation of red spider mite and yet show very different degrees of leaf damage; thus an attack of mites causing severe bronzing of Early Victoria appears to have very little effect on Bramley's Seedling. Early Victoria has one definite layer of palisade mesophyll. The result of the mites feeding on the leaves of this variety is a layer containing numerous empty or partially empty cells next to the upper epidermis. These empty cells fill with air and show up as the white speckling on the upper surface. As they die off, the coagulated contents in the corners of the cells turn brown, hence the bronzing of the leaves. Bramley's Seedling leaves, suffering a similar attack of mites, do receive the same amount of damage, but as they have two definite layers of palisade mesophyll, the damage to the lower layer is masked by the undamaged layer above. On the other hand, Worcester Pearmain also has two definite layers of palisade mesophyll, but damage shows up earlier on its leaves than on those of Bramley's Seedling, and it is liable to suffer from a certain amount of leaf drop after a bad attack of mites, which has never been observed with Bramley's Seedling.

SUMMARY.

A detailed account of the Fruit Tree Red Spider Mite, *Metatetranychus ulmi* (Koch), in the South-East of England is given.

Details of the synonymy and distribution of the mite are set out. The valid name is now considered to be *Metatetranychus ulmi* (Koch), and the mite has been recorded from all the deciduous fruit-growing areas of the world except South Africa. It is most serious as a pest in the South-East of England, but it is becoming more persistent in other areas also.

There are considered to be five chief factors influencing populations of the mite; these are: (1) The number of generations in each season, which in Essex and Kent has been five. (2) The action of the predator population. A detailed study was made of the relationship between the winter eggs of the mite and the predacious activities of various insects in the autumn. (3) The effect of weather conditions. Warm weather increases the metabolism of the mite. (4) Effect of spray programme. No really efficient spray has yet been found and many cause increases in the mite population. (5) Dispersal phase of the mite, which causes the mite to move from one orchard to another.

The various stages of the mite, winter and summer eggs, larva, protonymph, deutonymph and adults are described, and a method of distinguishing the stages by the number and situation of the ventral setae is shown. Females always have one larval and two nymphal stages before becoming mature, but males may have one larval and one or two nymphal stages. The habits of the mite, including feeding, the formation of webbing, and copulation, are considered. The factors affecting the hatching of winter eggs are discussed.

A method for breeding the mites in the laboratory is described. Figures for immature and adult life of mites of both sexes for each generation from 1947 to 1949 are given. The average number of eggs laid by females was 11. The complete life cycle takes 26 days. The ratio of males to females is discussed.

A study of parthenogenesis has been made. Unfertilized eggs always mature into males. The influence of parthenogenesis on the life cycle is considered.

In the literature there are records of the mite on over 80 species of plants; the authors have found it on all the common cultivated deciduous fruits and on 12 species of trees and shrubs from hedgerows and gardens. Eleven species of orchard weeds have also been found with the mite on them. There is no wholly resistant variety of apple or plum, but Bramley's Seedling and Victoria plum are less seriously damaged than are other varieties.

The external and internal damage to the leaves is described and considered. The mouthparts of the mite and their mode of action are described.

ACKNOWLEDGMENTS.

The authors thank Dr. A. M. Massee for his great help during all these investigations. The Agricultural Research Council, The Associated Fruit Growers of Essex, Ltd. and the Pettar Society have all helped during the work and this is gratefully acknowledged. They also thank Mr. M. D. Austin of the Field Laboratory for his assistance, Dr. R. S. Pitcher for drawing Figs. 6-8, Dr. S. C. Pearce for help in analysing the data for Figs. 10 and 11 and Mr. J. Taylor for analysing the biological data.

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PLATE I.

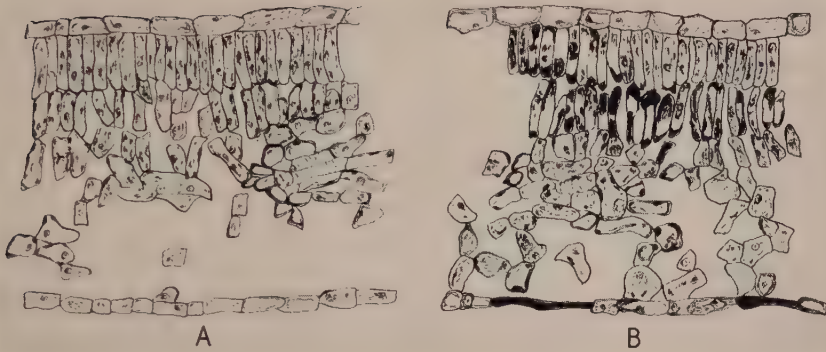


FIG. 12.

Sections of apple leaves. A. Normal. B. Damaged by feeding of the Fruit Tree Red Spider Mite, *Metatetranychus ulmi* (Koch).

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STUDIES ON PLANT GROWTH-REGULATING SUBSTANCES

IV. THE ACTIVITY OF CERTAIN ARYLOXY ACIDS FOR INDUCING ROOTING AND FOR TOMATO SETTING

By DAPHNE J. OSBORNE, R. L. WAIN and RUTH D. WALKER
Wye College (University of London)

SYNOPSIS.

A wide range of synthetic chemicals has been prepared and examined for activity in promoting the rooting of cuttings and for inducing seedless development of tomato fruits. In rooting experiments, both tomato leaves and privet cuttings were used as test material.

The results are examined and it is shown that in the main they conform to suggestions previously put forward concerning growth-regulating activity in relation to chemical structure.

INTRODUCTION.

The aryloxyalkylcarboxylic acids form an important group of growth-regulating substances and certain of these have proved useful in promoting rooting of cuttings (4, 5, 6, 7, 15) and for setting tomatoes (3, 15, 17, 21, 27, 32, 33). Although compounds effective for rooting, such as α -naphthylacetic acid and indole-3-acetic acid and for tomato setting such as 2-naphthoxyacetic acid are now in use on a commercial scale, there is still the possibility that better materials remain undiscovered owing to the almost unlimited number of compounds in this group.

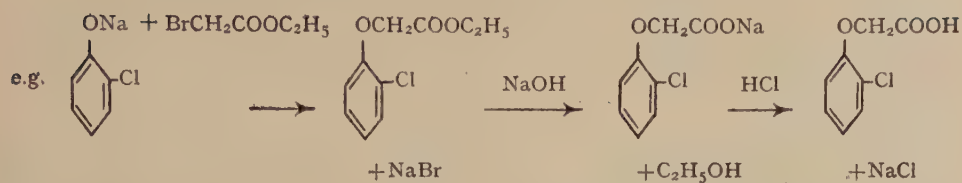
The short route to the discovery of better materials is probably an academic study of chemical structure in relation to growth-regulating activity, a subject which has already received considerable attention (6, 8, 19, 20, 23, 24, 25, 26, 29, 31). Investigations along these lines have been proceeding at Wye for several years and a large number of aryloxy acids have been synthesized and submitted to various biological tests. It is the purpose of this paper to present the results obtained in rooting and tomato parthenocarpy investigations. Similar studies relating to the activity of these compounds for setting pomaceous fruit, and for producing morphogenic effects in the tomato plant have been the subjects of separate publications (14, 13).

MATERIALS AND METHODS.

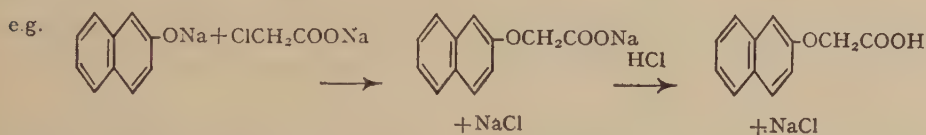
Preparation of chemicals.

One of the following standard methods was employed for the preparation of the aryloxy acids used:

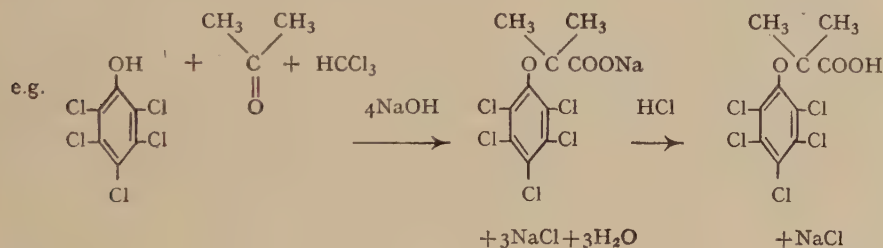
Method I (23). By condensation of the sodium salt of the appropriate phenol with the ethyl ester of a mono-halogen substituted fatty acid in alcohol solution. Subsequent hydrolysis with aqueous alkali, followed by acidification, yielded the acid, which was then crystallized to sharp melting point.



Method II (30). By condensation of the sodium salt of the phenol in aqueous solution with the sodium salt of the appropriate mono-halogen substituted fatty acid; the crude acid obtained on acidification was purified by crystallization.



Method III (1). The α -aryloxyisobutyric acids were prepared by condensation of acetone, chloroform and the respective phenol in the presence of solid sodium hydroxide. After heating under reflux for some 5-6 hours, water was added and the mixture was heated for a further period to effect hydrolysis; the crude acid was then obtained by acidification and was purified by crystallization.



The tomato leaf rooting test.

This test, devised by Hitchcock and Zimmerman (4), was employed as a quick and useful sorting test for determining the rooting capacity of synthetic growth-regulating substances. Very low concentrations of an active growth substance are usually adequate to produce a rooting response. Young tomato leaf cuttings, placed with the basal end in water and kept under glasshouse conditions, normally produce roots within 4-6 weeks, whereas if such cuttings are pre-treated with root-inducing substances, rooting may occur within 2 weeks.

Each cutting used in the tests described here was the fourth leaf from the apex of a healthy tomato plant, the leaves being, as far as possible, of uniform size and not exceeding 6-7 in. in length. The lower 2½ in. of each cutting was immersed for 24 hours in an aqueous solution of the sodium salt of the growth substance under test. Control cuttings were placed similarly in distilled water. Cuttings were then washed and set out in beakers of tap water with the basal 3-4 in. immersed and were grown in a greenhouse.

The final records for the test were taken when the control cuttings had just started to produce roots.

The privet rooting test.

Hitchcock and Zimmerman (4, 6, 7) used semi-lignified cuttings of privet as a test object with satisfactory results. Cuttings used here were taken from wild privet (*Ligustrum vulgare* L.) when the current year's growth was 3-4 in. long; this was found to be about the second week in May. Flowering shoots were avoided and nodal cuttings 3 in. long were used. The cuttings were treated as described above for tomato leaves and, after washing, were set out in boxes of sand. They were grown in an electrically heated frame.

Root counts and measurements were carried out after about 5 weeks, when the control cuttings had just begun to root.

Assessment of parthenocarpic activity.

Zimmerman and Hitchcock (30) and Gustafson (3) were among the first to show that a set of seedless fruit may be induced in tomatoes following a single application of 2-naphthoxyacetic acid to the open flower truss. In subsequent investigations Zimmerman and Hitchcock (e.g. 32, 33), using self-sterile tomato varieties, have assessed the parthenocarpic activity of a wide range of compounds by this method. Luckwill (9) has used measurements of rates of growth of parthenocarpic fruitlets to obtain a quantitative comparison of the activity of different compounds.

In the tests described here, self-fertile varieties were used and it was therefore necessary to emasculate the blossom before pollen was mature; only blossoms from the first and second trusses were treated. Some 10 days after emasculation, during which the ovaries became receptive, blossoms were sprayed with an aqueous solution of the sodium salt of the compound, containing a wetter of the sodium secondary alcohol sulphate type at 1/300. The ovaries and calyces were thoroughly wetted with the spray which was applied with a hand atomiser.

RESULTS.

Assessment of rooting activity.

Detailed records of root development on both tomato leaves and privet cuttings were made; these included the number of cuttings rooted for each concentration of each substance; the number of roots per cutting and the total root length per cutting.

In the tomato leaf rooting test these figures were used to calculate the "rooting capacity" for each treatment. Indole-3-butyric acid was taken as the standard treatment with a rooting capacity of 100; the rooting capacity of any treatment compared with the standard then became:

$$100 \times \frac{\% \text{rooted} \times \text{Total root length on all cuttings in the treatment.}}{\% \text{rooted} \times \text{Total root length on cuttings treated with indole-3-butyric acid.}}$$

For these detailed results, reference should be made to Osborne (11).

In the privet test, similar records were made but the compounds were compared with the untreated controls on a basis of percentage rooted and number and

average length of roots per rooted cutting. Indole-3-butyric acid was found to give somewhat variable results on privet. In one year's tests the fresh weights of the detached roots were recorded in an attempt to bring into consideration the thickness of the roots and the amount of lateral root growth. These figures, recorded by Walker (28), are available for reference.

Detailed results are not presented here, but in Table I the range of concentrations studied has been given, together with the concentration found effective for definite rooting activity. Few compounds tested appeared to be entirely without effect, so only considerable stimulation of either the length or the number of roots, or both, has been treated as significant.

Assessment of parthenocarpic activity.

A full record of percentage fruit set was made and fruit weight and size were also recorded in most of the tests. Measurements of the rate of growth of the young parthenocarpic fruitlets were not found to give any useful information; indeed, the rate was remarkably constant, though the final size attained by the fruits was to some extent dependent on the chemical used.

Various types of fruit development were encountered in these experiments. Emasculated blossoms, left with no further treatment, were often found to develop small seedless fruits, completely devoid of green gelatinous matter. These fruits, of which the diameter rarely exceeded 3 cm., were considered "dry sets" on account of their similarity to the "dry set" common in normal tomato-growing under conditions not conducive to fertilization of ovaries. In certain trials, usually at the end of the season with slow growing plants, such development was found to be suppressed. The growth of these plants was abnormal, the foliage being tough and very dark green, while on the upper surface of the leaf midrib numerous buds appeared at the base of the leaflets; these eventually grew out to form sturdy new shoots. It was also found that seed development in the normally fertilized tomatoes from the same batch was considerably reduced. These symptoms correspond closely to those described by Blencowe and Caldwell (2) for outdoor tomatoes infected with a new virus disease called Aspermy. It is possible, therefore, that certain plants in some of our trials indoors may have been suffering from this disease. When effective tomato-setting compounds were used on these plants an unusually high proportion of partially hollow fruit was produced. In view of these results it would seem important that in testing for parthenocarpic activity, plants suspected of having this disease should be rejected.

The fruits produced, when healthy emasculated ovaries were sprayed with a substance possessing parthenocarpic activity, were usually found to be similar to normal tomatoes in shape and size. They contained no fertile seeds, but the undeveloped ovules were surrounded by the normal layer of green gelatinous matter which in most instances, completely filled the fruit. The diameter of these fruits was about 5 cm. Only this type of fruit was regarded as indicative of parthenocarpic activity.

A few of the compounds tested, although inactive in inducing parthenocarpy, were found to prevent or reduce the development of "dry set" fruits. In many such instances the ovaries became yellow and abscised.

All these results are detailed by Walker (28) and Osborne (11).

A summary of the parthenocarp results, with range of concentrations tested and range effective for the production of good-sized fruits, well filled with gelatinous material, is presented in Table I.

DISCUSSION.

Of the many compounds examined, few have shown greater activity than that of established materials although several new compounds have exhibited a comparable degree of activity. Results of root-inducing experiments were often variable and two tests did not always give consistent results. Also, with certain compounds in the privet rooting test, it was found that results from experiments in the two separate years were not in agreement. Thus, in the first year indole-3-butyric acid which was used as a standard, gave poor results, whilst in the second year it was among the most active of the compounds tested.

An important consideration in these investigations is the possibility that roots produced as a result of treatment may not continue to develop; further, subsequent growth of the cutting may be affected. It is, therefore, necessary to grow the cuttings for some time before the activity of the treatment can be properly assessed. In general, these factors have not been investigated in the present work so that, as far as practical recommendations are concerned, our results can only form the basis for further experiments.

Although it is impossible to predict the rooting activity of a substance on a certain species until it has been tested on that species, results on privet and tomato leaves might indicate which compounds merit further investigation. In a trial carried out at Wye by Miss B. Hardt on the rooting of gooseberry cuttings, several compounds were included on the basis of the present results; of these, 2:4:5-trichlorophenoxyacetic and α -(2-naphthoxy)propionic acids gave good results. The performance of the other compounds, however, was disappointing.

Cabbage leaf cuttings have been successfully rooted using growth substances also selected on the basis of the present results. In a trial carried out in the College Horticultural Department by Miss E. Keep, the following treatments gave most satisfactory results using the 24-hour soak method.

α -(2-chlorophenoxy)propionic acid (5 p.p.m. and 15 p.p.m.).

α -(2-naphthoxy)propionic acid (5 p.p.m.).

α -(2:4:5-trichlorophenoxy)propionic acid (0.5 p.p.m. and 2 p.p.m.).

α -(2-methyl-4-chlorophenoxy)propionic acid (0.5 p.p.m. and 2 p.p.m.).

Of these, the trichloropropionic acid treatment at 2 p.p.m. gave the best results; roots were produced more quickly and more profusely than in other treatments. This treatment has been adopted in the Department as a standard procedure for effecting vegetative propagation of cabbage.

In another trial carried out here by Miss M. Page, using yew cuttings, good results were obtained following treatment with 1:3-bis(carboxymethoxy)benzene, a compound which we have consistently shown to be active at 25 p.p.m. in the privet rooting test (Table I). The activity of this substance, which contains two oxyacetic acid side chains, is of interest in connection with studies on chemical structure in relation to growth-regulating activity.

In the fruit setting experiments on tomato, a substance which possessed the

capacity to stimulate parthenocarpic development, usually gave good, even, well-shaped tomatoes, which were well filled with green gelatinous material surrounding the undeveloped ovules. Unsprayed emasculated ovaries on healthy plants developed into small, often partially hollow, fruits with no gelatinous layer.

Occasionally, however, this control development was suppressed. In such instances, other plants within the same experiment which were sprayed with an active fruit setting substance were found to produce a large number of partially hollow fruits. Usually, where this occurred, the growth of the plants was abnormal and it is probable that they were infected with Aspermy (2). In such tests it was impossible to assess activity. It is of interest to note that Swarbrick (21) encountered similar conflicting results which may perhaps be explained in this way.

Less than half of the 70 compounds tested were active in producing parthenocarpic tomatoes. Of these α -(2:4-dichlorophenoxy)-*n*-butyric acid, α -(1-naphthoxy)propionic acid and α -(2-naphthoxy)propionic acid were rated as at least equal to 2-naphthoxyacetic acid in their capacity to produce seedless fruit of good quality and about twelve other compounds were considered only slightly less effective. 2:4-dichlorophenoxyacetic, 2-methyl-4-chlorophenoxyacetic and 2:4:5-trichlorophenoxyacetic acids were all active at much lower concentrations than was 2-naphthoxyacetic acid but produced fruit of inferior quality.

A few of the compounds which exhibited no parthenocarpic activity caused abscission of undeveloped ovaries when sprayed on the plants at high concentrations. Substances showing this type of activity were bis-(4-chlorophenoxy)acetic acid (500 p.p.m.), bis-(2:4-dichlorophenoxy)acetic acid (200 and 500 p.p.m.), β -(2-naphthoxy)propionic acid (500 p.p.m.), α -(2-naphthoxy)*isobutyric* acid (500 p.p.m.).

In addition, the following treatments were found to prevent or reduce the normal control development of ovaries on healthy plants: β -(2-naphthoxy)propionic acid (250 p.p.m.), β -(1-chloro-2-naphthoxy)propionic acid (250 p.p.m.), α -(1-chloro-2-naphthoxy)propionic acid (250-500 p.p.m.), sodium 2-naphthoxymethane sulphonate (100-200 p.p.m.).

The results in Table I do not enable detailed correlations to be made of chemical structure with biological activity, though it is interesting to note that, in general, our findings do not conflict with the various suggestions previously put forward. The majority of the compounds studied possess the basic chemical configuration laid down by Koepfli *et al.* (8) and Went (29) for growth-regulating activity in the Went pea test. Since many of our compounds were inactive, however, it is evident that, for the types of activity considered here, other structural features might be important.

Muir *et al.* (10), using the *Avena* elongation test, have suggested that 2:6-substitution in phenoxyacetic acids is inconsistent with activity (see also 18). Our findings that 2:6-dichlorophenoxyacetic, 2-phenyl-6-chlorophenoxyacetic, 2:4:6-trichlorophenoxyacetic, 2:4:6-tribromophenoxyacetic, 2:4:6-triiodophenoxyacetic, 2:4-dichloro-6-methylphenoxyacetic, 2-methyl-4:6-dinitrophenoxyacetic and 2:3:4:5:6-pentachlorophenoxyacetic acids are inactive for parthenocarpic activity, lends some support to this possibility. Similarly, the negligible activity shown by all α -aryloxy*isobutyric* acids in these tests is consistent with the suggestion put forward from this Department (12) that, for certain types of growth-regulating activity, the presence of at least one hydrogen atom attached to the carbon atom adjacent to the carboxyl group of the side chain, might be important.

All β -substituted propionic acid derivatives examined were found to show negligible activity (Table I). These results were not unexpected in view of the possibility put forward by Synerholm and Zimmerman (24) that a β -oxidation mechanism of such compounds might operate within the plant, leading to their conversion to the inactive parent phenol.

SUMMARY.

A range of more than 70 compounds has been synthesized for testing as plant growth-regulating substances. Some of these materials have been previously examined by other workers.

For assessing capacity to induce rooting, both tomato leaves and privet cuttings were used as test material, using the 24-hour soak method. A number of compounds were found to possess marked rooting activity and although certain of these have been shown to be active on other species, the limitations of the results presented are recognized.

In assessing capacity to induce the parthenocarpic development of tomato fruits, compounds were sprayed as solutions of their sodium salts, together with wetting agent, on to emasculated tomato flowers. Several of the compounds were rated as being as effective as 2-naphthoxyacetic acid in inducing the development of good quality seedless fruit. The results for parthenocarp are briefly discussed in relation to chemical structure of compounds and it is shown that, in the main, they are not inconsistent with generally accepted views.

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TABLE I
Activity of aryloxyalkylcarboxylic acids in inducing rooting (Tomato and Privet) and parthenocarp (Tomato).

Compound and melting point	Rooting activity.				Refs. to previous workers.	Parthenocarpic activity		Refs. to previous workers.
	Tomato leaf rooting test		Privet rooting test.			Concentration range investigated and effective concentration for parthenocarpic activity.* p.p.m.	Remarks	
	Concentration range investigated and effective concentration for rooting activity.* p.p.m.	Remarks	Concentration range investigated and effective concentration for rooting activity.* p.p.m.	Remarks				
<i>Phenoxyacetic acids</i>								
Phenoxyacetic acid m.p. 95-96° C.	0.5-20	negligible activity			6, 7	250	inactive	32
2-chlorophenoxyacetic acid m.p. 147-148° C.	0.5-20	negligible activity	10-100 50-100	slight activity	0, 7	100-200 150	good quality fruits	32, 33
4-chlorophenoxy-acetic acid m.p. 157-158° C.	0.5-10 0.5-1	very slight activity reduced rooting at 10 p.p.m.	5-50 10-20	good sturdy roots	0, 7	5-50 20-50	excellent setting, quality of fruit variable—good in some tests, coarse in others	32, 33
3-methylphenoxy-acetic acid m.p. 101-103° C.	1-20	negligible activity						
2-phenylphenoxy-acetic acid m.p. 98-100° C.	0.5-20	negligible activity	20-100	results inconsistent in two tests		200-500	inactive	
4-phenylphenoxy-acetic acid m.p. 187-188.5° C.			20-200 20	good rooting activity		100-500	inactive	
4-tertbutylphenoxy-acetic acid m.p. 84-85° C.	10-20	negligible activity				50-250	inactive	
4-teramylphenoxy-acetic acid m.p. 62-63° C.	10-20	negligible activity				50-250	inactive	
2, 4-dichlorophenoxy-acetic acid m.p. 138-140° C.	0.1-1 0.1	cutting damaged at 1 p.p.m.	0.5-10 0.5-10	active	6, 7 15, 16	2-10 2-5 250	coarse fruits, sometimes hollow; modification of leaves	17, 19, 32, 33, 22
2, 6-dichlorophenoxy-acetic acid m.p. 133-135° C.							inactive	21, 18
2-methyl-4-chlorophenoxyacetic acid m.p. 110° C.	0.1-1 0.1	very good at 0.1				1-5 1-5	coarse fruits, sometimes hollow; modification of leaves	22
3-methyl-4-chlorophenoxyacetic acid m.p. 178-180° C.	1-20	negligible activity				5-25 5-25	active	
3, 5-dimethylphenoxyacetic acid m.p. 187-188.5° C.	1-20	negligible activity				100	highly active at 100 p.p.m. Good quality fruits	
2, 5-dimethylphenoxyacetic acid m.p. 113-115° C.	1-20	negligible activity				100	inactive—morphogenic effects developed	32, 33, 34
3-methyl-5-methylphenoxyacetic acid m.p. 129-131° C.	1-20	negligible activity				100	inactive	
2-phenyl-4-chlorophenoxyacetic acid m.p. 160-161° C.			20-200 20-50	severe damage to cuttings at 200 p.p.m. reduction of rooting. Concentration too high reduction of rooting		100-500	inactive	
2, 4, 5-trichlorophenoxyacetic acid m.p. 152-153° C.	0.1-1 0.1-1	optimum concentration 0.5	5 5		7 7	1-5 1-5 250	active	32, 33
2, 4, 6-trichlorophenoxyacetic acid m.p. 174-180° C.							inactive	32, 33
2, 4, 6-tribromophenoxyacetic acid m.p. 205-206° C.						250	inactive	
2, 4, 6-triiodophenoxyacetic acid m.p. 231-232° C.						250	inactive	
2, 4-dichloro-0-methylphenoxy-acetic acid m.p. 176-178° C.						250	inactive	
3, 5-dimethyl-4-chlorophenoxy-acetic acid m.p. 147-148° C.	0.5-10	negligible activity			7	20-250 50 100 100	very good	
2, 3, 5-trimethylphenoxyacetic acid m.p. 124-127° C.	1-20	negligible activity					very good	
2-methyl-4, 6-dinitrophenoxy-acetic acid m.p. 182-183° C.							inactive	
pentachlorophenoxyacetic acid m.p. 199° C.					7	250	inactive	
<i>β-phenoxypropionic acids</i>								
β-phenoxypropionic acid m.p. 97-98° C.	1-100	negligible activity				250	inactive	
β-(2, 4-dichlorophenoxy)-propionic acid m.p. 92-94° C.	0.5-10	negligible activity	20-100 20-100	considerably increased root growth in one experiment only		50-500	inactive	
<i>α-phenoxypropionic acids</i>								
α-phenoxypropionic acid m.p. 114-114.5° C.	0.5-20	negligible activity			6, 7	10-250	very good	32, 33
α-(2-chlorophenoxy)-propionic acid m.p. 113-5-114.5° C.	0.5-10 5-10 0.5-10	good, even, early rooting poor activity	1-50 5-10 0.5-10	numerous roots; fang- ing at high strengths few long roots; fang- ing at high strengths	7 7 7	10-50 25-50 10-50 25-50	very good inferior quality fruits	17, 32, 33, 27
α-(4-chlorophenoxy)-propionic acid m.p. 114-5-115.5° C.	0.5-10 0.5-10 0.5-10		0.5-10 0.5-10 0.5-5	numerous good roots reduction at 10 p.p.m.	6, 7 6, 7 6, 7	5-75 25-75 10-50 10-50	very good highly active at 50 p.p.m. Some root initiation on stem	17, 32, 33
α-(2-methyl-4-chlorophenoxy)-propionic acid m.p. 94° C.	0.1-1 0.5	good sturdy roots damage at 1 p.p.m.					highly active at 50 p.p.m.	
α-(2, 4, 5-trichlorophenoxy)-propionic acid m.p. 179-181° C.	0.1-1 0.5-1	good sturdy roots	5	reduction of rooting at 5 p.p.m.	6, 7	1-50 10-50	highly active at 50 p.p.m.	32, 33
<i>α-phenoxy-n-butyric acids</i>								
α-phenoxy-n-butyric acid m.p. 80° C.	0.5-10	negligible activity			6, 7	10-250 25-50 25-50	very good	32, 33
α-(2-chlorophenoxy)-n-butyric acid m.p. 81-5-82.5° C.	0.1-5 1	good even sturdy roots					very good	32, 33
α-(4-chlorophenoxy)-n-butyric acid m.p. 77-78° C.	1-10 5	slight activity			7	10-150 250	weak activity	32, 33
α-(2, 4-dichlorophenoxy)-n-butyric acid m.p. 80-5-81° C.	0.5-10 10	fairly good activity			6, 7	10-100 25-50 25-50	excellent	32, 33
α-(2-methyl-4-chlorophenoxy)-n-butyric acid m.p. 87-88° C.	0.1-5 0.5	good sturdy roots						
α-(2, 4, 5-trichlorophenoxy)-n-butyric acid m.p. 142° C.	0.1-5 1-5	good sturdy roots			7	10-50 50	highly active	32, 33
<i>α(phenoxy)isobutyric acids</i>								
α(phenoxy)isobutyric acid m.p. 97-97° C.	0.5-20	negligible activity				250	inactive	
α-(2-chlorophenoxy)-isobutyric acid m.p. 72-74° C.	0.5-20	negligible activity				250	inactive	
α-(4-chlorophenoxy)isobutyric acid m.p. 117-118° C.	0.5-20	negligible activity				250	inactive	
α-(2, 4-dichlorophenoxy)isobutyric acid m.p. 45-46° C.	0.5-20 20	low activity				250	negligible activity small fruits produced	
α-(2-methyl-4-chlorophenoxy)isobutyric acid m.p. 83-84° C.	0.5-20	negligible activity				100-250	inactive	
α-(2, 4, 5-trichlorophenoxy)isobutyric acid m.p. 92-93° C.	0.5-20	negligible activity				100-250	negligible activity	
<i>Other phenoxy acids</i>								
α-phenoxyphenylacetic acid m.p. 107-5-108° C.	1-20	negligible activity				100-250	inactive	
α-(2, 4-dichlorophenoxy)-phenylacetic acid m.p. 132-133.5° C.	0.5-10	negligible activity				100-250	inactive	
phenoxymalonic acid (Na salt) 2, 4-dichlorophenoxy-malonic acid (Na salt)	10-20 10-20	negligible activity negligible activity				375 375	inactive inactive	
bis-(4-chlorophenoxy)-acetic acid m.p. 141-143° C.			5-150 5-10	optimum 5 p.p.m. reduction of rooting above 10 p.p.m.		200-500	inactive—caused abscission at 500 p.p.m.	
bis-(2, 4-dichlorophenoxy)acetic acid m.p. 151-154° C.			1-150 1-5	slight activity reduction above 5 p.p.m.		200-500	inactive—caused abscission at 500 p.p.m. and 200 p.p.m.	22
1, 3-bis(carboxymethoxy)-benzene m.p. 195-197° C.	0.5-20	negligible activity	10-200 25	considerably improved rooting		200-500	inactive	
1, 4-bis(carboxymethoxy)-benzene m.p. 244-245° C.	0.5-20	negligible activity	20-200 20	not very good		100-500	inactive	
<i>1-naphthoxy acids</i>								
1-naphthoxyacetic acid m.p. 192-193.5° C.	0.5-10	negligible activity				100-250 250 250	weak activity	
β-(1-naphthoxy)-propionic acid m.p. 144-145° C.	0.5-10	negligible activity					inactive	
α-(1-naphthoxy)-propionic acid m.p. 150-151° C.	0.5-10	negligible activity				10-250 50	excellent	
α-(1-naphthoxy)-n-butyric acid m.p. 110-5-111.5° C.	0.5-10	negligible activity				50-250 250	small fruits, weak activity	
α-(1-naphthoxy)isobutyric acid m.p. 127° C.	0.5-20	negligible activity				250	inactive	
<i>2-naphthoxy acids</i>								
2-naphthoxyacetic acid m.p. 155-156° C.	0.5-10 5-10	some fasciated roots at 10 p.p.m. good roots at 5 p.p.m.	10-100 20-50	more roots at 50 p.p.m. and longer roots at 20 p.p.m.		10-100 25-50	very good	3, 17, 21, 30, 32, 33, 27
β-(2-naphthoxy)propionic acid m.p. 143-144° C.			20-100 20	considerably increased root growth		50-500	inactive; damage and abscission at 500 p.p.m. prevented dry set at 250 p.p.m.	
α-(2-naphthoxy)propionic acid m.p. 106-107° C.	0.5-10 1-10	some damage and fasciation at 10 p.p.m.	10-100 20-50	variable activity; damage at 100 p.p.m.		10-150 25-50	very good	32, 33, 27
α-(2-naphthoxy)-n-butyric acid m.p. 123-5-124° C.	0.5-10	negligible activity				50-250 250	weak activity	
α-(2-naphthoxy)isobutyric acid m.p. 122-123° C.	0.5-20	negligible activity				50-500	inactive; some abscission at 500 p.p.m.	
α-(2-naphthoxy)-n-valeric acid m.p. 117-118° C.	0.5-10	negligible activity	10-100	some increase in length of roots; doubtful activity		50-500	inactive	
α-(2-naphthoxy)-phenylacetic acid m.p. 152-153° C.	0.5-10	negligible activity				10-50 25-50	very good	
2-naphthoxymalonic acid (Na salt)	0.5-20 20	weak activity				375 375	weak activity	
1-chloro-2-naphthoxyacetic acid m.p. 165-166° C.			10-100 10-50	slight improvement in rooting		50-500 250-500	very slightly active; inferior fruit	
1, 4-dichloro-2-naphthoxyacetic acid m.p. 187-188° C.			10-200 10-50	large number of good roots; damage at 100 and 200 p.p.m.		50-500 500	very slightly active; small inferior fruit	
β-(1-chloro-2-naphthoxy)-propionic acid m.p. 170-171° C.			10-100 10-50	variable effect but some activity		250-500	inactive; reduced development of "dry set" fruits	
α-(1-chloro-2-naphthoxy)-propionic acid m.p. 171-173° C.			10-100 20	very large number of small to medium roots		100-500	inactive; prevented normal "dry set" at 250 and 500 p.p.m.	
2-thionaphthoxyacetic acid m.p. 78-80° C.			10-100 10-20	increased length of roots		100-300	inactive	
sodium 2-naphthoxy-methane sulphinate			20-200 20-200	slight activity over whole range		100-500	inactive: reduced normal "dry set" development	
sodium β-(2-naphthoxy)-methane sulphinate			20-200 100-200	slight activity		100-500	inactive	
2, 7-bis(carboxymethoxy)-naphthalene m.p. 217-219° C.			20-200 50-200	moderate activity		100-500	inactive; whole plant yellow at 500 p.p.m. reduced "dry set" at 100 p.p.m.	

* The effective concentration range for rooting and parthenocarpic activity is stated in italics in each case.

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GROWTH-INHIBITING AND GROWTH-PROMOTING SUBSTANCES IN RELATION TO THE DORMANCY AND AFTER-RIPENING OF APPLE SEEDS

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SYNOPSIS.

Recent work has suggested that the dormancy shown by the seeds and buds of many temperate zone plants may be due to the action of specific growth-inhibiting substances. The experiments described were designed to test this hypothesis, with particular reference to apple seeds which will not germinate until they have been after-ripened at a temperature just above freezing point for 60-70 days. Extracts made from different parts of the seed were tested by observing their effects on the growth of isolated sections of young oat coleoptiles under standardized conditions. These tests showed that the outer layers of freshly harvested apple seed do, in fact, contain relatively high concentrations of a growth-inhibiting substance, which disappears during the after-ripening process. Low temperature treatment, however, does not appear to be essential for the disappearance of the inhibitor, though it may be essential for the production of growth-promoting substances which appear in the embryo towards the end of the after-ripening process. In addition, it is suggested that moist conditions are necessary for the leaching out of growth-inhibiting substance from the seed coat.

INTRODUCTION.

THE seeds of the apple, in common with those of many other temperate zone plants, will not germinate until they have been after-ripened by holding them under moist conditions at a temperature just above freezing-point for a period of 60 to 70 days. In commercial practice, after-ripening is accomplished by packing the seeds between layers of moist sand or peat out-of-doors, where they are subjected to the normal low temperatures of winter, or, more efficiently, by keeping them under similar conditions in cold storage at the optimum temperature of 5° C. These treatments are referred to under the general name of stratification.

An essentially similar type of dormancy is shown by the buds of deciduous trees and shrubs, which require a period of winter low temperatures to break their rest-period and to ensure vigorous growth in the spring. Where the winter is insufficiently cold, bud break is delayed and irregular, and subsequent growth is weak, a phenomenon often encountered in deciduous fruit trees in warm climates.

Many investigators have studied the nature of the chemical and physiological changes which occur during the after-ripening period of dormant seeds and embryos, particularly in those of Rosaceous species. These investigations, which are reviewed by Crocker (5), have shown that low-temperature stratification is always accompanied by a marked increase in enzyme activity, particularly of catalase, peroxidases, oxidases and lipase, and probably also of proteases. At the same time there are changes in the stored food reserves of the seed: fats are converted into sugars, and insoluble proteins into soluble proteins, amino acids and other organic nitrogenous compounds. Such activation of enzymes and mobilization of storage substances, however, are the necessary precursors of germination in all seeds, whether they

require a period of after-ripening, or are capable of germination immediately after removal from the fruit. In the latter type of seed, the enzyme systems become active as soon as the seed is placed under conditions favourable for germination, whereas in the former type there would seem to be factors present in the freshly harvested seed which prevent these biochemical changes, thus holding the seed in a state of dormancy. Alternatively, it may be postulated that the dormant seed lacks some factor which is necessary for enzyme activity and growth, and that the period of low temperature stratification is necessary for the production of this growth-promoting factor.

Recent work on naturally occurring growth-inhibiting substances has drawn attention to the possible part played by such substances in controlling the dormancy of seeds and buds. Thus, Hemberg (6) has shown that the dormancy of freshly harvested potatoes is associated with the occurrence in the periderm of relatively high concentrations of an ether-soluble substance which inhibits cell elongation in the *Avena* coleoptile, and that the disappearance of this inhibiting substance coincides with the end of the rest-period. Treatment of the tubers with ethylene chlorohydrin, which breaks their rest-period, also leads to the disappearance of the growth-inhibiting substance. Similar results were obtained with extracts of the winter buds of *Fraxinus*, the dormancy of which is broken either by a period of low temperature or by ethylene chlorohydrin (7).

Moreover, the juices of many fleshy fruits have been shown to contain specific germination inhibiting substances, or blastocholines, the biological function of which is to prevent the germination of the seeds inside the fruit (8). The blastocholine present in tomato juice has recently been identified by Akkerman and Veldstra (1) as a mixture of caffeic and ferulic acids. Not only do these substances prevent the germination of tomato and other seeds, but they also inhibit the growth of coleoptiles and roots.

Barton and Solt (3), using a test based on the growth of wheat roots in solution, found that extracts of after-ripened *Sorbus* seeds were less toxic than extracts of dry seeds, though they could find no definite relation between the degree of root inhibition and the progress of after-ripening of the seeds. In lettuce seeds, the dormancy of which is broken by a period of dry storage, the disappearance of inhibiting substances was noted after a period of 8 weeks storage, and in two varieties this decreasing inhibitor content was paralleled by the increasing germinating power of the seeds. In a third variety, however, there appeared to be no relationship between the rest-period of the seed and the concentration of inhibiting substances. As a result of their extensive experiments these authors conclude "that dormancy is not imposed, solely, by the presence of a substance soluble in water and deleterious to the growth of wheat roots in solution. There may, however, be other substances, such as those which might be removed by long leaching, causing failure to germinate".

During work on the changes in the auxin content of the apple seed during the growing season it has been observed that, after the cessation of the "June drop", there is a steady accumulation of growth-inhibiting substances in the seed which tends to mask the activity of the naturally occurring auxin as measured in the tomato ovary test. Extracts of mature seeds are strongly inhibitory and no auxin can be detected in them. The present investigation was undertaken to determine what part, if any, these growth-inhibiting substances might play in inducing the dormancy of the mature apple seed.

EXPERIMENTAL METHODS.

Seeds of the apple variety Crawley Beauty were used for these experiments. Ether extracts were made of the embryos, endosperms and testas and the growth-promoting or growth-inhibiting activity of these extracts was then measured by observing their effects on the elongation of isolated sections of *Avena* coleoptiles. Such sections, prepared as described below, contain sufficient residual auxin to cause them to increase in length by about 50 per cent. in 24 hours when floated on water and kept at 25° C. In the presence of inhibiting substances growth is reduced

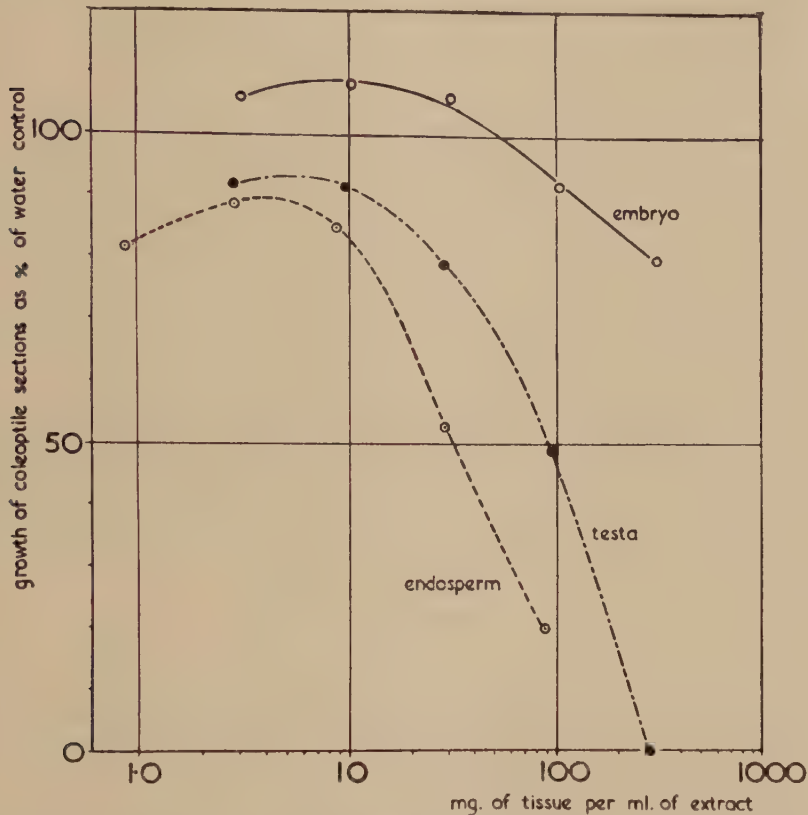


FIG. 1.

Effect of extracts of different parts of freshly harvested apple seeds on the growth of sections of *Avena* coleoptiles.

or completely stopped, whereas in the presence of auxins it may be increased by as much as 60 per cent. of the length reached by the water controls.

Methods of preparing extracts. Fifty seeds of the sample to be tested were dissected, the embryos, endosperms and testas being placed in three separate flasks and covered with 30 ml. of peroxide-free ether. The extraction flasks were then placed in a refrigerator at 4° C. After 24 hours and 48 hours the ether was poured off and replaced with a fresh lot of 30 ml. The total length of the extraction period

was 71 hours. The ether extracts were then taken to dryness in small specimen tubes and each was taken up in 5 ml. distilled water. The concentration of this extract was thus equivalent to 10 seeds per ml., and from this was prepared a series of dilutions corresponding to 3.3, 1.0, 0.33 and 0.10 seeds per ml.

Method of growing coleoptiles. After removal of their husks, seeds of Victory oats were soaked for $2\frac{1}{2}$ hours in water and were then placed on damp filter paper in petri dishes and kept in an incubator at 25° C. for 46 hours. By this time the seeds had sprouted and a uniform sample was selected for planting out in moist sand in dark boxes made of zinc. In order to assist the straight growth of the coleoptiles, each seed was planted at an angle of 30° to the vertical, with the coleoptile pointing upwards. Planting was done in diffuse daylight in the laboratory, after which the boxes were placed in the incubator for a further period of 29 hours. The coleoptiles had then reached a length of 15 to 20 mm. and were ready for use.

Method of carrying out assay. By means of a two-bladed knife a single section 2 mm. in length was cut from each coleoptile at a distance of 6 mm. from the tip. The leaf was pushed out from the centre of each section and the hollow coleoptile cylinders threaded in groups of ten on sealed glass capillaries, 7 cm. in length and 0.5 mm. diameter, each section being separated from the next by a small glass cylinder about 1 mm. long. Each capillary with its ten mounted coleoptile sections was then floated on the surface of 2.5 ml. of the test liquid contained in a glass boat. The boats were placed in petri dishes lined with damp filter paper and incubated at 25° C. for 24 hours. The coleoptile sections were then measured under a low-power microscope using an eyepiece micrometer. The mean elongation of each group of ten sections was expressed as a percentage of the mean elongation of the control sections growing in distilled water. This percentage was then plotted against the logarithm of the concentration of the extract, expressed either as mg. fresh weight of tissue per ml., or as seeds per ml. From the variations between replicate groups of ten sections it is estimated that differences less than 15 per cent. cannot be considered significant.

RESULTS.

Distribution of inhibiting substances in different parts of the seed.

The mature apple seed consists of three main parts. The embryo, with large fleshy cotyledons containing the bulk of the stored food reserves, is surrounded by a thin white membraneous layer of endosperm tissue. This, in turn, is enclosed within the hard testa from which it is separated only with some difficulty.

Extracts of these three seed parts show that the highest concentration of inhibiting substances, on a fresh weight basis, occurs in the endosperm; lower concentrations are found in the testa, and the lowest in the embryo itself (Fig. 1). The relative concentrations of inhibitor in these parts are roughly in the ratio of 30:13:1. The relatively small inhibitory effect of the embryo extracts is of interest in view of the fact that embryos excised from non-after-ripened seeds do, in fact, possess limited powers of growth, whereas embryos enclosed within the endosperm and testa, or within the endosperm alone, remain completely dormant until they have been after-ripened. If such excised non-after-ripened embryos are placed on moist filter paper at 25° C., the cotyledon in contact with the filter paper enlarges and turns green within a few days; in addition, 2-3 per cent. of the embryos

may show limited growth of the radicle after a period of 7-10 days. If non-after-ripened embryos are planted in moist peat, a considerable proportion of them may be successfully germinated though, compared with after-ripened embryos, growth is very slow and the seedlings are stunted with very short internodes and thick green leaves (5).

These observations suggest that the total dormancy of the embryo within the seed is partly due to the presence of the endosperm and testa. That the effect of

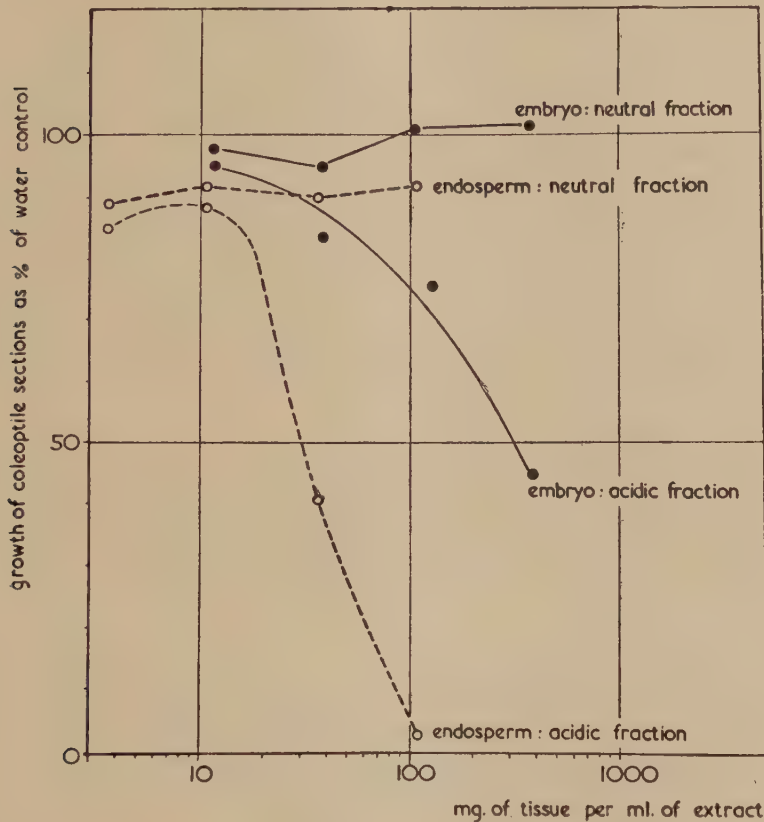


FIG. 2.

Effect of neutral and acidic fractions of embryo- and endosperm-extracts on the growth of sections of *Avena* coleoptiles.

these tissues on the embryo is a chemical one, and is not due to physical or mechanical causes, is shown by the fact that non-after-ripened seeds, of which the testas and endosperms have been ruptured or partially removed, still fail to germinate when they are kept under moist conditions at 25° C. Such facts are consistent with the hypothesis that the dormancy of the apple embryo is due partly to the high concentration of growth-inhibiting substances which occur in the outer layers of the seed, and partly to a much lower concentration of inhibitors in the embryo itself.

Acid fractionation of seed extracts.

Extracts of embryos and endosperms from freshly harvested seeds were fractionated by the method used by Boysen Jensen (4) for the purification of auxin extracts.

Sixty embryos or endosperms were extracted with ether for 71 hours as already described (p. 55). After drying over anhydrous sodium sulphate, the ether was removed by distillation, and the dry residue digested at room temperature for 2 hours with 10 ml. saturated glucose solution. The solution was then made alkaline with sodium bicarbonate and shaken three times with 20 ml. ether. The ether layer, containing the neutral and alkaline fractions, was separated and taken to dryness, whilst the aqueous layer was acidified with acetic acid and re-extracted with ether. This ether layer contained the acidic fraction, and was also taken to dryness. The dried extracts were taken up in water and tested as already described.

The results of this test are shown graphically in Fig. 2. No inhibiting substances could be detected in the neutral fractions, but the acid fraction of both the embryo and endosperm extracts strongly suppressed coleoptile growth. Confirmatory evidence of the acidic nature of the inhibitor is provided by the fact that it was found possible to adsorb it on the ion exchange resin known as Deacidite E. By shaking 10 ml. of seed extract with half its volume of Deacidite E for 1 hour, approximately four-fifths of the total inhibitor content was removed. By treating the resin with sodium carbonate, acidifying and re-extracting with ether, about two-fifths of the original quantity of inhibitor was recovered.

Attempts to break dormancy by chemical methods.

Tukey and Carlson have shown that the dormancy of non-after-ripened peach seeds can be broken by treatment with thiourea (10), but this method has proved unsuccessful when applied to seeds and excised embryos of apple. The seeds and embryos were treated by soaking them in thiourea solutions of concentrations ranging from 0.01-5 per cent. for a period of 24 hours before placing them on damp filter paper at 25° C.

Other substances which were tested over a wide range of concentrations in an attempt to induce germination without after-ripening included ethylene chlorohydrin, indolylacetic acid, water- and ether-extracts of yeast, peat extracts, and the cis- and trans-forms of 2 : 5 tetrahydrothiophene dicarboxylic acid.* The latter compound has been mentioned by Retovský and Horák (9) in a preliminary report as a substance which is particularly effective for inducing the growth of isolated plant embryos. Like all other chemical treatments that were applied, however, it proved ineffective on dormant seeds and excised embryos of apple.

Time required for after-ripening.

During October, about 3,000 seeds of the apple *Crawley Beauty* were collected, of which half were air-dried and stored in a bottle in the laboratory at an average temperature of 15° C. The other half, whilst still moist, were stratified between layers of damp filter paper and sand in a large crystallizing dish, which was kept in a refrigerator at a temperature of 4° C.

At intervals of about 10 days, samples were taken from both lots of seed and germination tests were carried out by placing 30 seeds in a petri dish, lined with

* The thiophene compounds were kindly supplied by Messrs. Pal Chemicals, Ltd.

damp cotton wool, which was kept in an incubator at 25° C. Counts of the number of seeds germinated were made at intervals of 2 days over a period of 2 weeks. Similar germination tests were carried out on batches of 30 excised embryos. An embryo was considered to have germinated as soon as it showed marked elongation of the radicle.

Germination of the seeds in petri dishes was not very satisfactory ; the proportion of seeds which germinated under these conditions never exceeded 25 per cent.,

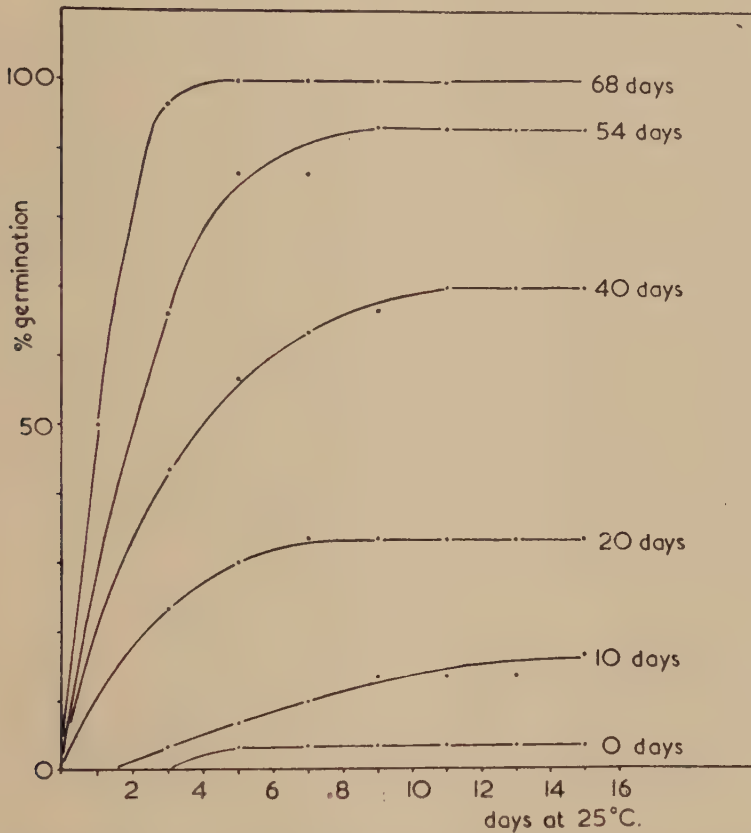


FIG. 3.

Progress of after-ripening of apple seeds kept under moist conditions at 4° C. as shown by the germination of excised embryos at 25° C.

even in samples which had been fully after-ripened, whereas similar samples planted in soil showed 100 per cent. germination within a few days.

It was found that the progress of the after-ripening treatment could best be followed by observing the germination of excised embryos. The results, presented graphically in Fig. 3, show that at least 68 days at 4° C. were required for full after-ripening. It was at this stage that the seeds first began to germinate in the refrigerator.

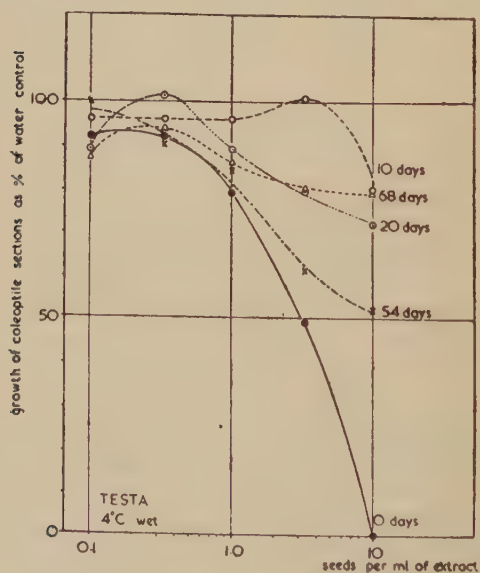
Seeds which had been kept in dry storage for periods up to 85 days showed no signs of germination, either in petri dishes or when planted in soil, and less than 2 per cent. of excised embryos showed any indication of radicle growth when placed on damp cotton wool at 25° C.

Effect of dry storage and after-ripening on inhibitor content of seed.

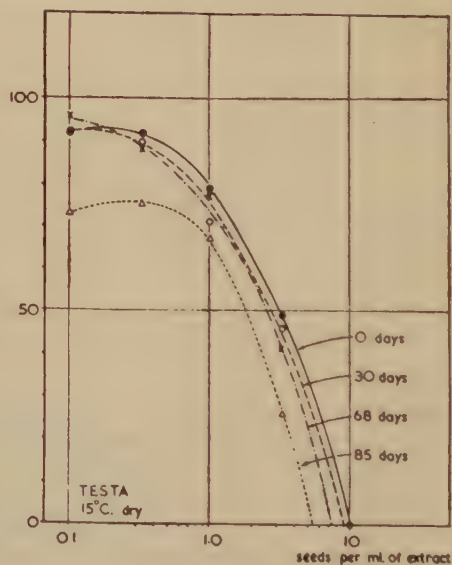
If the dormancy of freshly harvested apple seeds is, in fact, attributable to the presence of growth-inhibiting substances, it should be possible to demonstrate the disappearance of these substances from the seed during after-ripening at 4° C., but not during dry storage at room temperature. Accordingly, samples were taken at intervals of approximately 10 days from batches of seed stratified at 4° C. and kept in dry storage at room temperature, and ether extracts were made of embryos, endosperms and testas according to the method already described (p. 55). The influence of these extracts on the growth of *Avena* coleoptile sections is given in full in Appendix I, and in Table I is shown the per cent. inhibition caused by extracts containing the equivalent of five embryos, endosperms or testas per ml., as estimated from the smoothed curves. In Fig. 4, significant stages are shown graphically in order to illustrate the general trend in the inhibitor content of the seeds under the two conditions of storage.

It is convenient to examine the changes in the different tissues separately, though it must be remembered that the embryo, endosperm and testa are in close contact in the seed, and that water soluble substances can almost certainly pass from one tissue to another by diffusion, particularly under the moist conditions necessary for after-ripening.

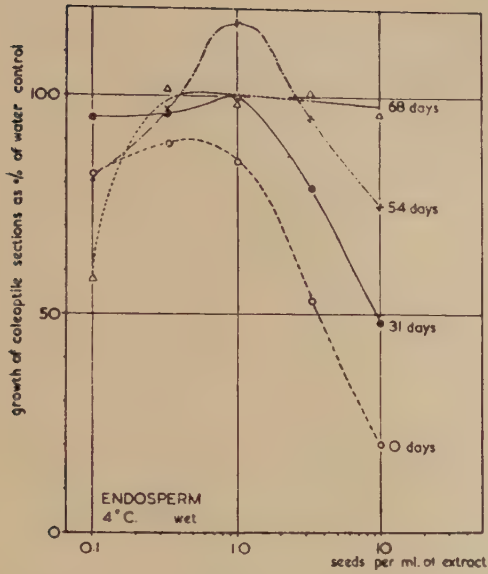
Testa. During the first 10 days of stratification there was a rapid disappearance from the testa of inhibiting substances, which subsequently increased again up till the 54th day, and thereafter showed a further decline (Fig. 4a).



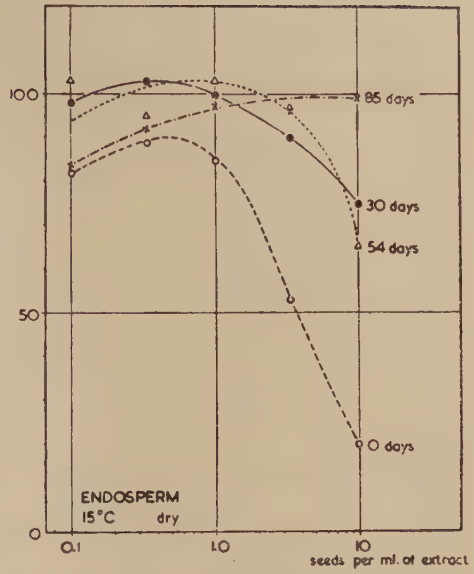
(a)



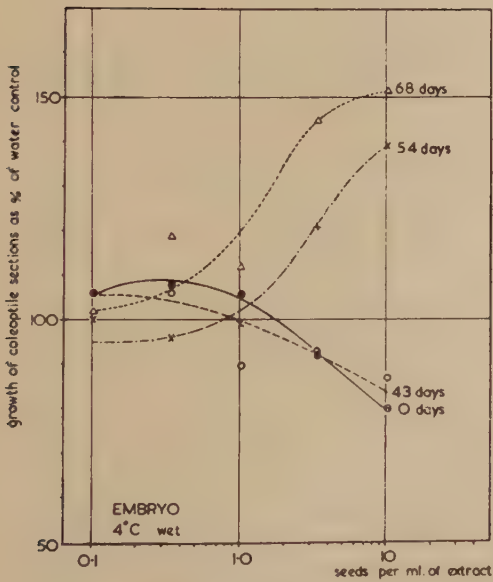
(b)



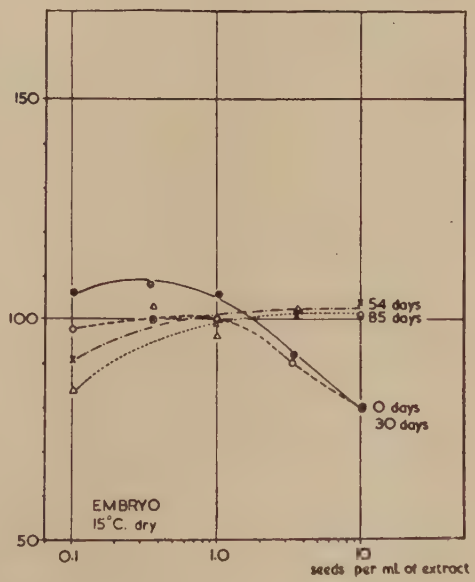
(c)



(d)



(e)



(f)

FIG. 4.

Effect of extracts of parts of apple seeds stored under two different conditions on the growth of sections of *Avena* coleoptiles.

TABLE I.

Estimated percentage inhibition of growth of Avena coleoptile sections caused by extracts of apple seeds of concentration = 5 seeds per ml.

Temperature and conditions of storage	No. of days	Embryo	Endosperm	Testa
4° C.—wet.	0	12	60	66
	10	21	69	2
	20	12	52	24
	30	16	32	18
	43	11	26	34
	54	—29	13	43
	68	—48	1	21
15° C.—dry.	0	12	60	66
	30	14	15	70
	43	—4	23	79
	54	—2	10	84
	68	—2	18	77
	85	—1	1	95

The initial rapid depletion of inhibitors from the testa was probably due to the leaching out of these substances under the moist conditions in which after-ripening was carried out. The subsequent increase, on the other hand, might have been caused by a movement of inhibitor from the endosperm into the testa along a concentration gradient.

By contrast, seeds in dry storage showed no diminution in the amount of inhibiting substances in the testa over a period of 85 days; during this time there was, in fact, a slight increase in the growth-inhibiting effects of the testa extracts (Fig. 4b).

Endosperm. In seeds stratified at 4° C. the growth-inhibiting effects of the endosperm extracts showed a steady decline over a period of 68 days, by which time they had practically disappeared (Fig. 4c). It is perhaps significant that about the same time was required for complete after-ripening of the seeds, as shown by the embryo germination test (Fig. 3).

However, the endosperms of the seeds in dry storage at room temperature also lost their growth-inhibiting properties (Fig. 4d). During the first 30 days the dry seeds actually lost more inhibitor than the stratified ones, but thereafter disappearance of the inhibitor proceeded somewhat faster in the latter group. After 85 days no inhibitor could be detected in the endosperms of the dry-stored seeds; nevertheless, the seeds were still completely dormant and the embryos excised from such seeds showed no signs of germination when placed on damp cotton wool at 25° C.

A curious feature of the endosperm extracts was that the lowest concentration tested, corresponding to 0.1 endosperm per ml., consistently proved more inhibitory to the growth of *Avena* coleoptiles than did higher concentrations corresponding to 0.33 or 1.0 endosperm per ml. After 68 days after-ripening, this lowest concentration was actually more inhibitory than the highest concentration of 10 endosperms per ml. This apparent reversal of the normal concentration/response curve is difficult to explain. It may perhaps indicate the presence of both growth-inhibiting and growth-promoting substances in the endosperm extracts, which at certain

concentrations might counteract one another, whilst at a lower concentration the inhibiting effect might predominate over the growth-promoting effect.

Embryo. As already stated, the dormant embryo contains relatively small amounts of growth-inhibiting substances and, during the first 43 days of after-ripening, little change in the inhibitor content can be detected (Fig. 4e). Nevertheless, during this period there is a considerable increase in the germinative capacity of the embryo (Fig. 3). At 54 and 68 days, however, the extracts of embryos from after-ripened seeds greatly stimulated the growth of coleoptile sections, indicating the presence of auxins.

On the other hand, no indication was obtained of any auxin formation in the embryos of seeds kept in dry storage for periods up to 85 days, although during this period there was an almost complete disappearance of inhibiting substances (Fig. 4f).

DISCUSSION.

The experiments reported above have demonstrated that the outer layers of freshly harvested apple seeds contain relatively high concentrations of an acidic substance, soluble in ether and water, which is capable of inhibiting cell elongation in sections of *Avena* coleoptiles.

They have shown also that this growth-inhibiting substance disappears when the seeds are kept under moist conditions at 4° C., and that the time taken for its disappearance, viz. 68 days, is also the time required to break the dormancy of the seed under these conditions. Moreover, when the seeds are stored under conditions which do not break their dormancy (e.g. dry storage at room temperature) no disappearance of the inhibitor from the testa can be demonstrated up to periods of 85 days, although during this time there is an almost complete disappearance from the adjacent endosperm tissue.

Although these observations suggest that this inhibitor may be a factor controlling the dormancy of the seed, the experiments with excised embryos indicate that it cannot be the only, or even the dominant, factor involved. As already pointed out, the factors controlling the dormancy of the apple seed must, to a large extent, reside in the embryo itself, in so far as excised embryos show only limited powers of growth until they have been after-ripened at low temperature. Yet, in these experiments, little or no relationship was found between the inhibitor content of the embryo and its capacity for growth, as is shown by the following observations :

(1) During the first 40 days of after-ripening there was a large increase in the rate of germination of the embryos (Fig. 3), but no detectable diminution in the inhibitor content of the embryo extracts (Fig. 4e).

(2) After 54 days in dry storage, no inhibitor could be detected in the embryo extracts but the embryos nevertheless still failed to grow when removed from the seed and placed under conditions favourable for germination.

The most outstanding difference between after-ripened and non-after-ripened embryos was not, in fact, the disappearance of inhibitor but the appearance of growth-promoting substances in the after-ripened seeds just prior to germination. No such growth-promoting substances were detected in the dry-stored seeds.

It is of interest to note that Avery *et al.* (2) found that auxin first appeared in the terminal buds of *Aesculus* and *Malus* about 3 weeks before the visible swelling of the buds, and that the highest concentration was reached just before bud-burst.

Since these buds also require a period of cold treatment to after-ripen them, the phenomenon would appear to be analogous to the appearance of auxin in after-ripened seeds.

In these experiments, no attempt was made to separate the growth-inhibiting and growth-promoting fractions of the extracts, and the technique employed measured only the combined action of these two factors. The shape of the curves suggests that in some instances both types of substance might have been present in the same extract, and the question therefore arises as to what extent the apparent disappearance of inhibitor might have been due to an increase in growth-promoting substances partially masking their effect. Such a possibility, however, in no way invalidates the results obtained: if both factors are, in fact, acting simultaneously, growth is presumably determined by the ratio of growth-promoters/growth-inhibitors, which is virtually what was measured by the technique employed.

In general it may be said that these experiments support the conclusion reached by Barton and Solt (3), that seed dormancy is not due solely to the presence of growth-inhibiting substances. They further indicate that low-temperature stratification, although not necessary for the disappearance of inhibiting substances from the embryo and endosperm, is necessary for the production in the embryo of growth-promoting substances, the appearance of which precedes, and is probably a necessary precursor of, germination. The moist condition, which is one of the requirements for the successful after-ripening of apple seeds, is probably necessary to remove growth-inhibitors from the testa. Unlike the embryo and endosperm, the latter is a dead tissue from which inhibitor appears to be removed by leaching, rather than by enzyme or other biochemical action.

This experiment suggests that three separate processes may be concerned in the after-ripening of apple seeds, viz.:

- (1) Disappearance of growth-inhibiting substances from the endosperm and embryo.
- (2) Leaching out of growth-inhibiting substances from the testa.
- (3) Formation of growth-promoting substances in the embryo.

Process (1) would appear to proceed irrespective of the temperature and moisture conditions under which the seeds are held; process (2) takes place only when the seeds are in contact with moisture; whilst process (3) requires either a period of exposure to low temperature, or moist conditions, or possibly a combination of both these factors. It should be noted that there is at present no evidence to show that processes (1) and (2) are in fact essential for the breaking of seed dormancy in the apple.

SUMMARY.

1. Ether extracts of mature apple seeds contain a substance which inhibits the growth of sections of *Avena* coleoptiles. The possible relation of this growth-inhibitor to the dormancy of the seed has been investigated.
2. In freshly harvested seed the relative concentration of growth-inhibitor in the endosperm, testa and embryo was in the approximate ratio of 30 : 13 : 1.
3. The inhibitor was shown to be acidic in nature.
4. During after-ripening under moist conditions at 4° C., disappearance of inhibitor from all parts of the seed was demonstrated. The time taken for its

disappearance was also the time required to break the dormancy of the seeds under these conditions, viz. 68 days.

5. In seeds stored dry at room temperature, the inhibitor disappeared from the endosperm and embryo, but not from the testa. Seeds stored under these conditions remained dormant indefinitely.

6. Growth-promoting substances appeared in the embryos of after-ripened seeds just before germination started. No growth-promoting substances were detected in the embryos of seeds in dry storage.

7. Attempts to break the dormancy of apple seeds by chemical treatments were unsuccessful.

8. Little correspondence was found between the germination capacity of excised embryos and their inhibitor content.

9. It is concluded that the formation of growth-promoting substances, rather than the disappearance of growth-inhibiting substances, may be necessary to break the dormancy of the seed.

APPENDIX I.

Effect of extracts of different parts of apple seeds (var. Crawley Beauty) on the growth of isolated sections of Avena coleoptiles.

Conditions and temperature of storage.	No. of days.	Part of seed extracted.	Concentration of extract (seeds/ml.) and coleoptile growth as % of control.				
			0.10	0.33	1.0	3.3	10
Freshly harvested seed.	0	Embryo	106	108	106	92	80
		Endosperm	82	89	85	53	20
		Testa	92	92	79	49	0
Moist. 4° C.	10	Embryo	124	121	101	95	60
		Endosperm	60	104	93	45	10
		Testa	96	96	96	101	80
	20	Embryo	100	110	101	98	75
		Endosperm	73	91	93	59	37
		Testa	89	102	89	80	72
	31	Embryo	115	112	107	87	81
		Endosperm	95	96	100	79	48
		Testa	98	104	92	88	38
	43	Embryo	106	106	89	93	87
		Endosperm	58	108	97	82	57
		Testa	95	98	80	75	32
	54	Embryo	100	96	98	121	139
		Endosperm	81	97	117	95	75
		Testa	100	90	84	61	52
	68	Embryo	102	119	112	145	152
		Endosperm	58	102	98	101	96
		Testa	87	94	86	80	79
Dry. 15° C.	30	Embryo	98	97	96	90	80
		Endosperm	98	103	100	90	75
		Testa	92	90	71	46	0
	43	Embryo	114	95	100	94	119
		Endosperm	87	102	98	83	66
		Testa	95	85	81	36	0
	54	Embryo	91	100	99	101	104
		Endosperm	103	96	103	97	65
		Testa	104	84	62	27	0
	68	Embryo	110	94	111	93	107
		Endosperm	94	97	103	89	67
		Testa	96	88	77	41	0
	85	Embryo	84	103	96	102	101
		Endosperm	84	92	97	76	99
		Testa	73	75	67	26	0

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REVIEWS

SCIENCE AND THE GLASSHOUSE. By W. J. C. LAWRENCE. (Edinburgh : Oliver and Boyd. 1950. 2nd edition. Pp. 175, illus. Price 15s.)

This book combines science and practice in a pleasant and easily understood manner, and should prove invaluable to all who are interested in crops grown under glass, and to all, including glasshouse builders, who are interested in glasshouses.

Tradition and practice have, in the past, largely dictated the methods to be used in horticulture ; in this book Mr. Lawrence has proved, under conditions comparable to those found in the average nursery to-day, that the methods handed down by our predecessors are not always the best, due, in some cases, to the influence of other factors which have also changed in recent years.

It is conveniently divided into sections, each of which has a concise summary. The first two sections give the latest information on basic problems, such as the ingredients of the right compost, partial sterilization of the soil, and the effect of cold water on seedlings in a moderate temperature. The third section is of a more scientific and experimental nature, and some of the conclusions drawn may have to be modified in the future as more information is forthcoming on the part played by light and position in the growth of plants. One point of importance to the practical horticulturist is that houses running East-West give greater light transmission than North-South houses during the propagating season ; apart from the saving in fuel during the hours of daylight, this effect, when linked with the fact that the care and treatment of plants in the seedling stage has a profound effect on their final growth and yield, is significant.

To those who intend building in the future, the information regarding choice of district, site, slope of the roof, etc., will prove of great value, especially from the economic aspect, which has become increasingly important in recent years.

M.M.M.

THE FRUIT YEAR BOOK, 1950. (London : Royal Horticultural Society. 1950. Pp. 160, illus. Price 8s. 6d.)

As is to be expected, that annual production of the Royal Horticultural Society, *The Fruit Year Book*, is packed with good things contributed by selected stars of the fruit-growing world, or at least of the scientific side of it. The fruit-consuming world is not represented.

Factors affecting fruit production are studied by A. Gavin Brown in connection with plums. He shows that some varieties secrete more nectar than others and are, therefore, more attractive to bees ; that hive bees intent on nectar can work some varieties without touching the stigma but do touch it when collecting pollen. Hive bees tend to keep to one particular tree and are of little use to pollinate self-incompatible varieties. Humble bees, on the other hand, with their longer hairs and clumsier movements collect and distribute pollen freely at every visit and, unlike

the honey bee, wander from tree to tree. Hence they are good pollinators for self-incompatibles as are blow flies, but not hover flies. Humble bees are less weather-conscious than hive bees and work longer hours. R. J. Garner writes on grafting in the garden, describing and illustrating side-, rind-, and bottle-grafting and rehabilitation by inarching.

V. H. Goldschmidt and A. V. Delap provide an adaptation from the German of Fey and Wirth on the spindlebush method of growing apple and pear trees. The spindle-trained tree stands half-way between a bush and a vertical cordon. It has no proper branch system. The fruiting wood does not issue from the main stem directly but from short branches depending from laterals and cut to a downward-facing bud to ensure horizontal elongation and less vigorous growth. Shoots are tied down and not summer-pruned and correct or incorrect tying directly influences the crop. Advantages claimed are early first bearing, small space required and easy transplantation up to ten years. Anyone who can master the complexities and still remain sane should get a lot of fun out of it, if not profit. The meticulous records of the cropping of his espalier and spur-pruned apple trees kept for the last twenty years by the late Mr. A. Hassard of Rathmines, are published and discussed by J. G. D. Lamb. Accurate data of this kind are scarce, especially for espaliers. Dr. A. M. Massee advises on the essentials of red spider control. Considering that one egg missed in winter could build up to 160,000 mites by summer and result in 4,000,000 eggs for overwintering, it is recommended that his words should not pass unheeded. "Some virus diseases of fruit trees in England," by L. C. Luckwill, discusses the symptoms of various virus diseases and their control in apples, pears, plums and cherries. The recognition marks are clearly described and illustrated and the whole provides a useful guide. H. Martin discusses the new phosphorus insecticides, largely the outcome of German work by Schrader. Certain of the compounds, when sprayed on to plants, are absorbed into the sap stream which becomes highly toxic to sucking insects. As for the fate of the human consumer of plant products thus treated, well, no one has actually died yet or, to put it more scientifically, "the residue hazards still require a final opinion".

A. Gavin Brown writes entertainingly on early views on "blight" as propounded in the horticultural literature of the time when it stood for almost any horticultural disaster not obviously traceable to human agency. C. Bould, in a paper on methods of applying nutrients to fruit trees, deals with soil injection, tree injection and foliage sprays. J. H. Jeffries has been experimenting in the protection of fruit against spring frosts by means of water spraying. His results indicate that a spray at the rate of one-tenth inch per hour will protect blossom against 16° F. of frost and one-twentieth inch against lighter freezes. A. Pollard describes how he made a palatable wine, clear, pale golden, clean and dry, from his own outdoor grapes, mainly Black Hamburg, and sugar saved from the domestic ration. In addition to palatability it possessed the "faculty of provoking conversation" and is clearly a product worth sampling. Mrs. D. J. Swithinbank describes and illustrates the difference between wasp and tomtit damage on apples and pears. Late-keeping pears were the subject of a lecture by T. E. Tomalin which is reprinted, as is a discussion by this speaker and H. H. Crane, on the selection of fruit for exhibition and the technique of showing. From other lands come notes on fruit-growing in Northern and Southern Ireland and in Sweden, and on peach pruning in the U.S.A.

G.St.C.F.

PESTS OF FLOWERS AND SHRUBS. By G. Fox Wilson. Bulletin 97 of the Ministry of Agriculture and Fisheries. (His Majesty's Stationery Office, 1950. Pp. 105, illus. Price 4s. 6d.)

This well-illustrated account of the insects that attack flowers, trees and shrubs, first published in 1937, has brought together information that was in many cases slight and was certainly scattered. As entomologist to the Royal Horticultural Society, Mr. Fox Wilson had both the experience and the background necessary for the preparation of the bulletin, and it has remained one of the standard works on the subject. It has now been revised and brought up-to-date and, with the comprehensive index, it occupies 105 pages and has 118 drawings and photographic illustrations.

The author first gives a short introductory account of insects and related creatures and then defines the principles of pest control. He covers cultural, mechanical, and biological methods and deals fairly fully with control by means of insecticides. The pests are described in detail. The account of general pests includes the biology and habits of slugs, wireworms, leather-jackets and other soil creatures that are continually troublesome to many garden plants. The section that deals with pests of lawns, roses, herbaceous borders and other special garden groups, including shrubberies and greenhouses, is of particular interest.

The text is both informative and readable. The illustrations deserve special praise for their photographic excellence, most of which has been retained in the reproduction. It should be noted that Fig. 39, used as an illustration of rose slugworm, is misleading because the insects represented are pear slugworms on a pear leaf; Fig. 47 is out of focus and not up to the general standard. As a new attempt at representing an insect's life cycle, Fig. 3 is interesting, but much detail is lost in reproduction at these sizes except in the case of the cockchafer where a near-success is achieved.

The bulletin will be welcomed by gardeners and nurserymen alike as giving them up-to-date information on a wide range of pests. The recent death of its author is a great loss to horticultural entomology.

H.W.M.

INDEX OF AGRICULTURAL RESEARCH IN PROGRESS, 1951. Agricultural Research Council. (London: H.M.S.O., 1951. Pp. 53. Price 3s. 6d.)

The foreword indicates yearly revision is contemplated. May we hope also for the yearly issue of this most valuable reference work?

While the horticulturist will probably find most of what he wants under the Crop index, the specialist may prefer to look under the Index headings (abbreviated):—Biochemistry, Entomology, Fertilizers, Insecticides, Plant Breeding, Plant Pathology, Plant Physiology or Weeds.

D.A.

OBSERVATIONS ON THE RASPBERRY CANE MIDGE (*THOMASINIANA THEOBALDI* BARNES)

I. BIOLOGY *

By R. S. PITCHER
East Malling Research Station, Kent

INTRODUCTION AND HISTORY.

THE genus *Thomasiniana* comprises three species the distribution of which is limited to Europe. Rübsaamen (1893) gave the original description of *Diplosis oculiperda* sp. n. Since that date the following generic changes have occurred: *Clinodiplosis* Kieffer, 1896, *Thomasia* Rübsaamen, 1910, and *Thomasiniana* Strand, E., 1916.

Although the genus belongs to the sub-tribe Trifila of the family Cecidomyiidae, or Gall Midges, none of its members are gall formers, as the larvae live under peeling or broken superficial tissue of the host plant, without causing cell proliferation.

T. oculiperda (Rübs.) is known as the Red Bud Borer because of its habit of invading budded stocks of roses and fruit trees, preventing the union of stock and scion.

T. theobaldi Barnes was first recorded by Theobald in 1921 as *Thomasia* sp. Barnes (1927) described it and named it the Raspberry Cane Midge.

T. crataegi Barnes was first found by Mr. H. C. F. Newton in 1937. Barnes (1939) described it and named it the Hawthorn Stem Midge.

The present investigation of the bionomics and control of *T. theobaldi* was begun in April, 1946, after reports of a high death rate of raspberry cane following injury by this species had raised the possibility of an association with the fungal disease known as Cane Blight, although the precise nature of the relationship between the two remained in doubt.

Although Theobald (1923) had referred to the midge as "a seriously increasing pest" it has been considered of little economic importance until comparatively recently. It has been noted as causing peeling of the rind and as possibly provoking branching in the growing cane (Barnes, 1931). Suggestions have also been made that it might be secondary to fungal or other damage (Barnes, 1931; Massee, 1940, and Fox Wilson and Green, 1944). In 1921, in the monthly reports to the Ministry of Agriculture, Theobald referred to "a subsequent attack by fungi which enter through the scars" causing 75 per cent. death of fruiting cane, but this unpublished record appears to have been overlooked until the present investigation. Theobald mentioned the midge frequently in the monthly reports until 1926, occasionally reporting complete loss of cane and subsequent grubbing of plantations.

From 1927 onwards there are few records of this species although Harris (1930) and Massee (1930) referred to a probable association between midge and fungus. In 1942 and 1943 severe attacks on raspberries at the Royal Horticultural Society's

* Part of a Thesis approved for the Degree of Doctor of Philosophy in the University of London.

Gardens at Wisley provided an opportunity for further work (Fox Wilson and Green, 1944). These authors were satisfied that there was an association between midge and fungus but were unable to decide which was the primary parasite. In typical cases of Cane Blight disease the fungus *Leptosphaeria coniothyrium* (Fckl.) Sacc. was known to behave as a wound parasite and it seemed possible that the midge could in some way provide it with a means of entry. However, Barnes (1944) showed that the midge too was dependent on broken epidermis for successful oviposition and larval development. Thus it appeared that a wound was a prerequisite of both midge and fungal attack and could offer equal opportunities to each. Nevertheless, the frequent association of serious midge and fungal attack and the consistently negative results of experiments with protective fungicides suggested that the midge was in fact playing the primary part. A study of the life history of the midge led to the discovery that certain features in the normal growth of the raspberry cane had an important bearing on midge biology and on the initiation of fungal attack. At the same time Mr. P. C. R. Webb of the Plant Pathology section at East Malling, was investigating the fungal side of the dual attack. The results of collaborative work on this aspect are described in Part II of this series. (See p. 95.)

DISTRIBUTION.

Previously, this species has been reported only from the counties of Kent, Surrey, Warwick and Worcester in England, and from Poland (Barnes, 1927 and 1931). The midge is unknown to many workers in Europe and North America, but its presence in Poland has been confirmed, and Thiem (1949) refers to a paper by Voss (1922) describing symptoms on raspberry canes in South Hanover which resemble very closely those observed in this country. More recently it has been discovered in Switzerland by Bachmann (1949) and it is possible that it may prove to be much more widespread. In England the midge has been found by the writer in Kent, Surrey, Sussex, Berkshire, Cambridge and Essex, but not in the Scottish raspberry-growing districts or in Nottinghamshire. It appears likely, therefore, that this species is confined to the southern half of the country, and even here it has been found only on cultivated raspberries.

EXTERNAL MORPHOLOGY.

Imagines.

The midges are typical members of the Cecidomyiidae, of a delicate structure and generally of a dark reddish colour. Barnes (1927) gives a full description. He cited several small points of difference between *T. theobaldi* and *T. oculiperda* but later, after examining more material, he concluded that there was no valid morphological distinction between them. Observations by the author agree with those of Barnes except for the figures of length. Measurements by the author are as follows. *Female*: Average of 20, 1.78 mm.—max. 2.16 mm.; min. 1.38 mm. *Male*: Average of 20, 1.42 mm.—max. 1.79 mm.; min. 1.25 mm.

In life the following colours may be seen: Antennae, dark brown; palpi, pale brown; face, buff; eyes, black; thorax, chitinated plates dark brown, remainder buff; halteres, amber; legs, buff, covered with dark hairs which are less dense near the joints; abdomen, reddish brown, covered with dark hairs.

Eggs.

The eggs are translucent, shiny and approximately elliptical in longitudinal section. The dimensions of 25 eggs averaged 0.328×0.094 mm., with a maximum of 0.365×0.097 mm. and a minimum of 0.311×0.090 mm.

Larvae.

In the course of their growth the larvae change considerably, both in general appearance and in morphological characters, although at all stages they are typical legless cecidomyids. When newly hatched they are translucent and barely visible to the naked eye, approximately 0.4×0.095 mm. in size. When fully fed they may reach a size of 3.5×1.0 mm. and are either pink or orange in colour. Three larval instars occur, the morphology of which will be described elsewhere. The bilobed sternal spatula is not present before the final moult.

Pupae.

Pupae are found within the cocoons constructed by the larvae. They bear the cephalic and thoracic horns typical of most cecidomyids. For most of their life they are coloured like the larvae, darkening shortly before emergence. The dimensions of 30 pupae averaged 1.56×0.58 mm., with a maximum of 1.99×0.79 mm. and a minimum of 1.24×0.46 mm. The cocoons showed a corresponding variation, averaging 2.13×1.14 mm.

BIOLOGY.

The first account of the biology of this species was that of Barnes (1926), who found midges in early July and larvae in July and August. Massee (1940) noted two flights of midges, the first in May-June, and the second in July-August. Fox Wilson (1944) described the occurrence of three larval peaks in the field in June, July and August, 1943, while Barnes (1944), studying material from the same source in the insectary, found that three generations occurred in 1944, with midges emerging 9th May to 3rd June, 14th July to 8th August and 25th August to 17th September. Midges emerged between 17th September and 8th October from larvae taken from the field in late August, a fact which suggests the occurrence of at least a partial fourth generation. All these authors agree that the larvae live in the outer tissues of first-year raspberry canes, falling to the ground and entering the soil when fully fed. Barnes (1944) further showed that eggs are laid only where the epidermis of the cane is broken.

In the present investigation, field observations during the summer of 1946 were coupled with a study of the life history in the laboratory. In the following two summers population counts made in the field and supported by observations on caged material confirmed and elaborated the picture of a multivoltine cycle presented by Barnes (1944). It was also confirmed that the midges oviposited only on broken tissue and that the larvae fed superficially on the canes and when mature fell to the ground, forming a cocoon and pupating therein. The pupae in due course left the cocoons and made their way to the surface of the soil before the midges emerged.

The details of population fluctuations and of the biology of individuals are given below. Those aspects of the biology which are intimately affected by certain features of the growth of the raspberry cane are considered separately. (See p. 80.)

Life cycle.

Technique. The laboratory studies on life history in 1946 were carried out on the progeny of single pairs of midges, which were confined in small cages. It was found possible to rear the larvae successfully on cut first-year canes of raspberry. Slits were made in the outer cortex in which the females readily laid their eggs. The canes were then stood in water, into which the larvae fell when fully fed. They were then transferred to a flower pot containing soil covered with a layer of peat, and the emerging midges were trapped in a lamp glass. The data agree quite closely with those obtained under field conditions.

The length of the summer life cycle varied from 26 to 49 days, being shortest when temperatures were high. No midges emerged in 1946 from eggs laid after 7th August; instead, the larvae over-wintered in the soil and emerged in an insectary between 5th and 30th May. Their life cycles varied from 226 to 298 days.

In 1947 and 1948 the life cycle was studied with caged material in the field. The temperature in these cages approximated very closely to the shade temperature outside. Summer life cycles varied from 24 to 55 days in 1947 and 33 to 75 days in 1948, a markedly cooler year. The life cycle of over-wintering individuals varied from 258 to 274 days in 1947-48 and 251 to 309 days in 1948-49.

Generations.

In 1946 biological observations were made at 11 field sites, each of which supported a substantial midge population. Eggs, first found on 9th May, were always present until 17th September, and some larvae could always be found from 21st May until mid-October. It was evident, therefore, that an overlapping of generations was occurring. Two well-marked larval generations were discerned, the second much larger than the first; at Lingfield they occurred approximately on 15th June and 2nd August. There was no clearly marked third generation, but young larvae could be found up to mid-September, a fact suggesting that such a generation did occur and that it was smaller than the second.

In 1947 two plantations of the variety Newburgh were selected for systematic field population counts. That at Lingfield, Surrey, was established as a cane nursery soon after the variety was first introduced into this country from America about 17 years ago. In 1946 over 90 per cent. of the canes were attacked and it bore the highest observed population amongst the eleven sites visited. The Addington field, the stock in which originally came from Lingfield, had been a cropping plantation for several years and, in 1946, over 60 per cent. of the canes were attacked. Counts were usually made at weekly intervals on a representative sample of 50 first-year canes, with the results shown in Fig. 1. Three clear generations, shown by egg and larval peaks, occurred at Lingfield, each peak being bigger than the preceding one and at Addington a similar sequence occurred. The first series of field cages (referred to above) was inoculated with 2 to 4 females each, as soon as midges were available in the field. As the first midges emerged from this series the second was started and so on. Under these conditions four flights of imagines occurred as follows: 13th to 28th May, 17th June to 9th July, 25th to 30th July and 23rd August to 4th September. The times of the various life cycles were 33 to 55 days, 30 to 55 days, 24 to 37 days and 258 to 274 days, respectively.

In 1948 comparable population counts were made (Fig. 2). At Lingfield a hymenopterous parasite considerably reduced the numbers of the second and third

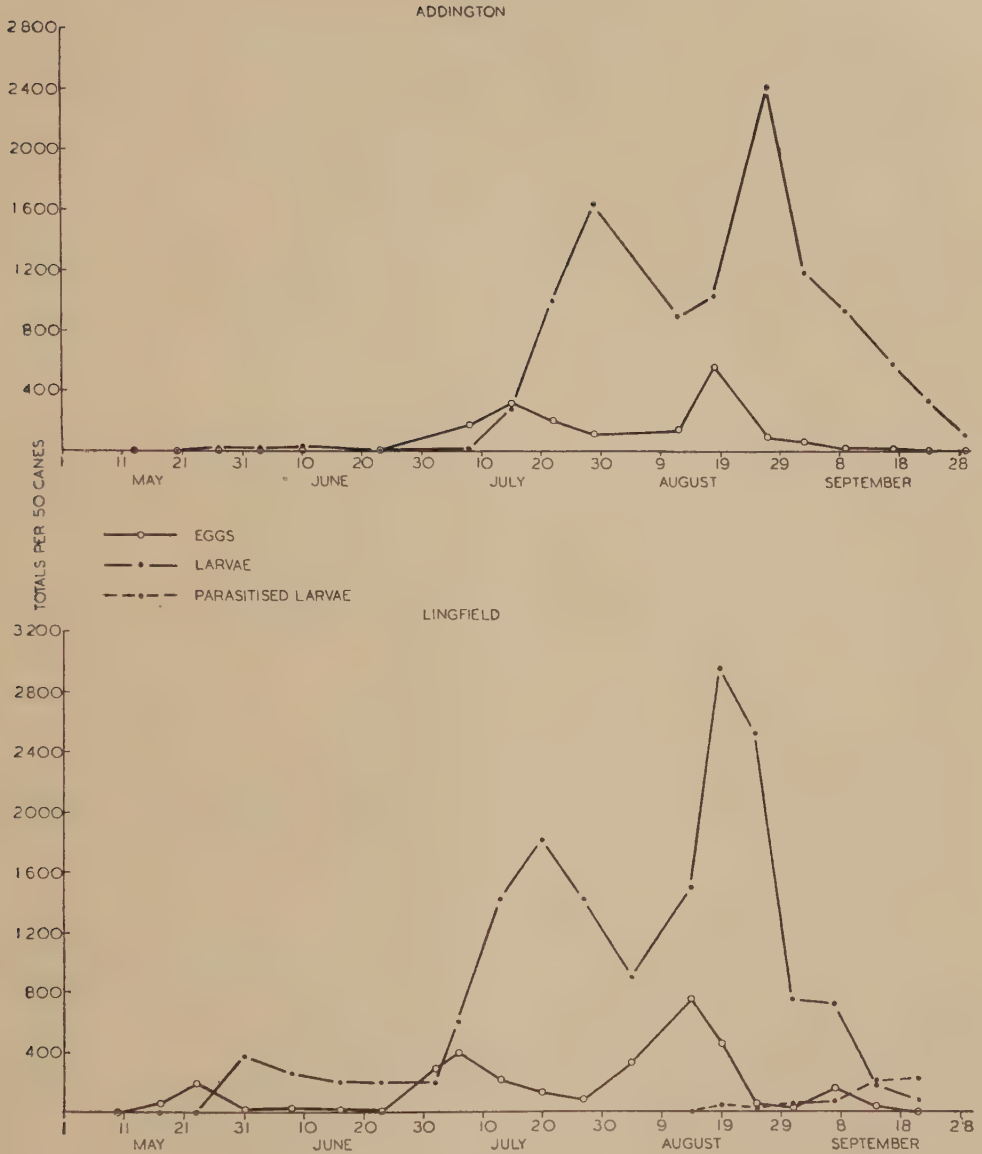


FIG. 1.
Population counts, 1947.

generations, and possibly altered their timing slightly; nevertheless, Generation 3 was clearly later than in 1947. At Addington three generations occurred but, again, Generation 3 was much later than in 1947 and had a smaller larval peak than Generation 2. In both fields Generation 1 was larger than in 1947. In 1948, field cages were again maintained, but a new series was not started until about half of



FIG. 2.
Population counts, 1948.

the midges from the previous generation had emerged, thus approximating more closely to the behaviour of the bulk of the field population. The times for Generations 1 and 2 were 52 to 75 days and 33 to 50 days respectively. About 25 per cent. of the latter and all of Generation 3 passed the winter as larvae in the pre-pupal stage, taking from 251 to 309 days to complete the cycle.

Discussion of population studies.

In comparing the seasons 1946 to 1948, account must be taken of their climatic differences. The summers of 1946 and 1948 were mainly cool and wet, with brief spells of very hot weather in early and late July respectively. The summer of 1947 was generally warm and dry, although the spring was late, following the severe winter. The duration of the spring emergence period varied from six weeks in the cool spring of 1946 to 2 to 3 weeks in 1947, when the May temperatures were abnormally high. In 1948 the emergence was more regular, extending over 3 to 4 weeks and rising to a sharp peak around 16th May, when the soil temperature at 4 inches rose to 64° F., the maximum for the month. The spring was early, following a mild winter.

Although the field population estimates of 1946 should not be compared too closely with the counts of 1947 and 1948, they showed a small larval generation in June followed by a much larger one in late July—early August. The third generation in September, was small. The 1947 Lingfield graph (Fig. 1) showed first and second generations conforming to the 1946 pattern, but the third generation was unexpectedly large and early. This was probably due to the unusually warm weather, which shortened the life cycles and encouraged many of the larvae of the second generation to pupate and emerge instead of remaining in the quiescent phase. At Addington the sequence was similar, except for the small size of Generation 1. This may have been due to the use of an alternative oviposition site on the fruiting canes as noted commonly in 1948. (See p. 83.) The whole sequence was 4 to 9 days later than at Lingfield, probably because of the greater altitude and northern aspect of the Addington field.

In 1948 the egg peaks of Generation 1 were a little later than in 1947, but were much larger on both fields, despite a smaller cocoon population in the soil. There were, however, many more oviposition sites available to the newly emerged midges. At Addington, Generation 2 was also larger than in 1947, although reaching its maximum at almost exactly the same date. Generation 3, however, was influenced by the cool summer, being smaller and occurring 2 to 3 weeks later than in 1947.

After the latter part of Generation 1, the Lingfield populations were greatly reduced by parasitism and cannot be regarded as strictly comparable with the others. Nevertheless the delaying effect of the cool summer on Generation 3 is clearly marked. Thus in 1948 both the climate and the behaviour of the midge resembled those of 1946.

It appears, therefore, that a small or medium-sized larval generation in late May and early June, followed by a much larger second generation in late July and early August, is a normal occurrence. The size and timing of the third generation varies considerably, depending on the effect of climatic conditions on the larvae of the second generation. In a normal year, many of these larvae over-winter and only a residue pass through a third generation. In an abnormally warm year such as 1947, the majority will pupate so that the third generation is likely to be large and the progeny of a few individuals may pass through four generations.

Imagines.

Midges have been found in the field between 30th April and 17th September and in the insectary from 27th April to 30th September. They are extremely delicate and, in general, short-lived. The following data have been obtained from field observation and from the laboratory studies carried out in 1946.

In the laboratory, some males live for five days but the majority for three days or less, only about one in five exceeding this time. Females tend to live longer, up to eight days, although only one in three survives beyond the third day. When egg laying is delayed for any reason, females tend to live longer.

Emergence is much affected by day-to-day climatic conditions, being inhibited by cool weather. If conditions remain favourable, it is usual for the bulk to emerge on 2 or 3 warm days. Midges emerge from a longitudinal split in the thorax of the pupae which have left their cocoons and assumed an upright position on the surface of the soil. With the wings still crumpled, the midges run actively about the soil, seeking a vertical surface large enough to enable them to hang, head uppermost,

while the wings expand. Once a suitable position is found the midge remains still, apart from spasmodic movements of the wings which expand in 2 to 5 minutes. Midges usually remain hanging thus for 20 to 50 minutes before attempting to fly. Emergence has been seen to occur at various times between 0900 and 1600 hours G.M.T. and twice-daily records taken in 1947 showed that the numbers emerging between 0800 and 1400 hours were approximately equal to those emerging after 1400 hours. These conclusions contrast with those of Barnes (1944), who considered the evening to be the typical emergence time.

Records of the sex of emerging midges show that, although there is a rough balance amongst large numbers (60 per cent. male : 40 per cent. female), individual females have a marked tendency to produce unisexual or nearly unisexual families. Of nineteen families reared in 1946-47, fourteen were unisexual and five showed a marked preponderance of one sex. This tendency has been noted by Barnes (1931, 1939 and 1944) in this and other species of *Thomasiniana*, and also in several other genera.

Flight usually lasts one minute or less, as the midges tend to seek the shelter of the host plant within 2 to 3 feet of the ground. Flight occurs freely in suitable weather conditions, but has not been observed before 0800 or after 2040 hours G.M.T. It is much influenced by temperature, occurring freely in calm conditions from 65° F. upwards but rarely below 60° F. In unfavourable conditions the midges rest on the leaves and canes of the raspberry and also frequently on strands of cobweb.

Copulation is brief (approximately 90 seconds) and may occur very soon after the female has emerged, even before the wings have expanded. Active males have, under favourable circumstances, a very acute perception of the presence of virgin females and in the field may congregate in a small cloud of 20 or more around cages and tubes containing them.

Oviposition may occur whenever conditions are favourable for flight. It has been observed between the hours of 1100 and 2040 G.M.T., being most frequent from 1500 to 1800 hours. With the exception of small numbers laid in the axils of leaves under laboratory conditions, all eggs found and all oviposition observed have been associated with broken epidermis. The female first explores the surface of the canes with regular movements of her antennae and when suitable tissue is detected, the ovipositor is utilized for a more detailed examination. Eggs may be laid singly or in a group, usually lying in close contact with plant tissue on both upper and lower surfaces. Most eggs are laid in freshly split tissue; dry splits or those already occupied by larvae are seldom used.

Eggs.

Eggs have been found in the field between 23rd April and 21st September. Laboratory data show that the numbers laid vary from 12 to 72, averaging 45 per female. Apparently the full complement of eggs is rarely laid, as gravid females have been found to contain 90 to 97 eggs. If conditions are favourable, most of the eggs are laid in the first 24 hours of life; 86 per cent. of 323 eggs from seven females were laid thus. The remainder are laid, a few at a time, on the second to the fourth day. In the field, most of the eggs are probably laid within the first few hours of life although low temperatures may delay oviposition for a day or more.

Hatching may take 2 to 7 days, depending on the temperature; at 70° F. it

takes place by the third day. The contents of the newly-laid egg are uniformly dense and fill the whole shell. At 70° F. a concentration towards the median line is apparent within 24 hours and, after 48 hours, clear signs of segmentation can be seen. Soon the ocular spots appear and movements become common. About one-third of the length from the posterior end, a brown pigmented spot appears, which becomes denser as hatching approaches and which persists in the larva for 1 or 2 days.

Larvae.

Larvae have been found in the field from 10th May onwards. After mid-September, when egg-laying ceases, larval numbers gradually decline. In the laboratory, larvae have lived for 9 to 49 days on the cane with average minima and maxima of 13 and 22 days. The numbers reaching maturity vary from 8 to 70, averaging 30 per female. Usually each instar occupies approximately one-third of the total larval life, although the length of Instar III may vary greatly. Overcrowding may cause some larvae to leave the cane before reaching full size, while lack of nourishment can prolong life. Larvae may be found under the peeling outer cortical tissues of first-year canes within a few millimetres of the spot where they hatched from the egg. Often they crowd together, lying in closely packed groups of up to 100 individuals with the ventral surface innermost, in contact with the cortical cells exposed by the splitting.

On hatching, the larvae tend to move into the splits until they meet a barrier in the form of intact outer cortical tissue. Here they lie singly or in groups of two to five and commence to feed, causing at first clearly defined dark brown spots on the green background of the cane (Plate I). The tissues immediately above and below the larvae are both discoloured. As the larvae grow and enter Instar II, the brown spots increase in size and when Instar III is reached they coalesce to produce a uniform brown to black area of tissue (Plate II).

The colonies produced by larvae of Generation 1 rarely reach 100 individuals per cane. The colonies of Generation 2 larvae may be much larger; over 450 individuals have been noted on a single cane, while 200 to 300 per cane occur quite commonly. Some of the Generation 3 colonies may be very large and overcrowded, often exceeding 300 larvae on one cane, while many other canes are almost free from attack.

When the third instar is reached the main population of larvae assume the typical pink colour but a few are of a yellow to orange colour. In all morphological characters these appear identical with the pink larvae, except for this clear difference in the colour of the fat body. There are no intermediate colour gradations. Midges reared from larvae of either colour appear to be identical and will interbreed, often producing larvae of both colours. Most of the recorded colour differences in cecidomyid larvae are gradual variations associated with environment. Sen (1938) and Koronéos (1939), however, note distinct colour differences in larvae of the same species. The percentage of orange larvae present under field conditions has varied from 5.3 to 10.1, averaging 7.2 per cent. in a total of 14,000. This difference persists in the pupae, which retain the larval colours.

When fully fed, the larvae move to the edges of the split and fall to the ground. A few of them may project themselves short distances by a feeble hopping motion, but this species is not capable of the vigorous jumps exhibited by some cecidomyid larvae.

Pupae.

On reaching the soil, larvae usually burrow below the surface within a few minutes and form a cocoon. In the summer, from 13 to 25 days may be spent in the cocoon, with an average of 17 days. The winter is spent in a quiescent condition in the cocoon, from 201 to 269 days elapsing before emergence. Under insectary conditions about half the larvae died during the period spent in the soil, and there are indications that a greater mortality may occur in the field. The distribution of the cocoons in the soil around the base of the cane largely depends on the random scattering of larvae during their fall. Larvae leaving canes in the laboratory were trapped on a sheet of cardboard coated with tree-banding grease. Approximately 90 per cent. fell within a 5 cm. radius. In the field, the falling larvae are frequently deflected by petioles and other obstructions but the same tendency exists, 71 per cent. being recovered within 5 cm. of the base of vertical isolated canes. It was found that most of the larvae pupate near the surface of the soil. In the laboratory, 92 per cent. of the cocoons were found in the top centimetre. Of 459 cocoons recovered from the field, 83 per cent. were in the top centimetre and 14 per cent. and 3 per cent. in the second and third centimetres respectively.

The cocoons are fairly tough and are covered with a layer of soil particles, which makes them difficult to detect without the aid of a washing technique. A small proportion (2.8 per cent. in 1,451 individuals) of naked pupae have been found in the soil samples. These pupae may have been removed from their cocoons in the process of breaking up the soil or they may have pupated without them. The latter possibility is suggested by the observations of Fox Wilson (1944) who found many naked pupae in the mulch at the base of the canes.

After the cocoon is completed, the larvae enter a quiescent phase in which they lie in a curved attitude with the ventral surface convex. The over-wintering larvae remain quiescent until the spring, but in the summer prepupal changes begin soon after the cocoon is formed. The most conspicuous feature of the early stages is a gradual lateral separation of the ocular spots. In normal active larvae and in quiescent larvae these lie on the median longitudinal axis with their inner, convex surfaces touching. In a summer trial carried out under laboratory conditions, the ocular spots began to separate on the third day after the larvae had entered the soil, reaching the outer margins of the body by the fifth day. Pupation took place on the seventh day and emergence on the sixteenth. In over-wintering larvae these changes in the relative position of the ocular spots begin shortly before pupation in the spring. In the late summer a steadily increasing proportion of the larvae halt their development at the quiescent stage, until finally no pupae can be found. A state of diapause does not appear to exist as emergence can be provoked in the winter within two or three weeks at a temperature of 70° F. without prior exposure to freezing temperatures.

BIOLOGY IN RELATION TO THE GROWTH OF THE RASPBERRY CANE.*Cane anatomy and cane splitting.*

At an early stage in the biological investigations it became apparent that oviposition, larval development and fungal attack were intimately bound up with the occurrence of splits in the outer cortical tissues of the first-year raspberry canes. As no information on the incidence of these splits was available, the following observations on their nature and occurrence were made.

The aerial parts of the raspberry (*Rubus idaeus* L.) are biennial, bearing fruit in their second season. The first-year canes appear above the ground in April and by early May they are 20 to 30 cm. high. At this stage they present in transverse section a typical vascular cylinder of pith, xylem, cambium and phloem surrounded by a ring of longitudinal pericycle fibre bundles (Fig. 5(a)). Outside this lies a layer of parenchyma and an epidermis. The outer parenchyma cells are appreciably smaller than the remainder. Within this parenchyma run five vertical ridges of more compact cells, three of which run into the base of each petiole. By late May the canes are approximately 50 cm. tall and a periderm is developing outside the pericycle. By early June, 4 to 5 layers of periderm cells have been produced and secondary vascular tissue is well developed (Fig. 5(b)). Growth continues until

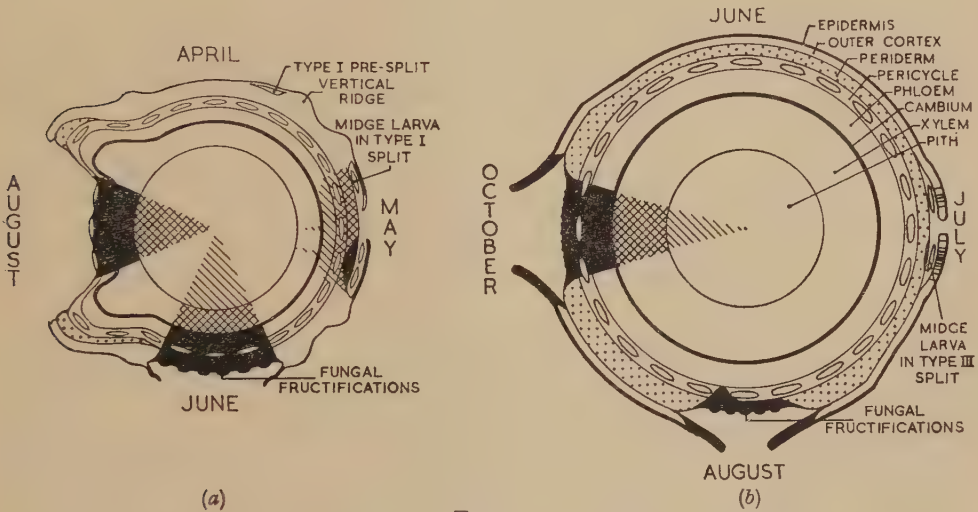


FIG. 5.

Diagrammatic transverse sections of raspberry cane illustrating the sequence of development of midge and fungal lesions.

(a) Generation 1.

(b) Generation 2.

late August, producing canes of 200 cm. and more in height and thickening the periderm layer to about 15 cells. These canes stand over winter and produce flowers on axillary laterals in the following spring, when they are known as fruiting canes.

At various stages in the growth of the first-year canes, three distinct types of longitudinal split occur. A factor common to all is the inability of the outer cortical layers to keep pace with the increase in girth of the cane. The type of split produced is dependent on the state of development of the outer cortical tissue.

Type I split. This split is characteristic of the early stages of growth of certain varieties in certain seasons. Splitting occurs first in late April, reaching a maximum in early May and ceasing by June. It is the shallowest type of split, involving the epidermis and the outer layers of the cortical parenchyma to a depth of 2 to 3 cells.

(Plate III.) This flimsy upper layer soon curls back and dries, but for about a fortnight it provides a moist and succulent cover eminently suitable for midge oviposition and larval development. The production of this split seems to depend on a separation of the outer layers which begins on either side of the vertical ridges. This condition may be seen macroscopically as a silvery area and is clearly visible in transverse section. (Fig. 5(a).) If the tangential tension is sufficient, a longitudinal split, which may be up to 6 cm. in length, occurs in the lifted layer. These splits appear most frequently below the nodes but may also be found internodally. On spiny canes the separation does not occur so readily.

On the varieties Newburgh and Malling Enterprise, Type I splits were common in 1946 and 1948, but in 1947 hardly any were to be found. The varieties Norfolk Giant and Malling Landmark produce few or no such splits at any time. The percentage of canes which split and the area of tissue affected on each cane do not approach those of the Type III split, nor do the splits arise in the same regular sequence. Type I splitting thus appears to be a rather irregular phenomenon, probably dependent on a combination of several growth conditions.

Type II split. A simple type of split penetrating radially from epidermis to pith. As it develops it gapes to a V-shaped section and then fills with callus. Usually the cortical layers do not separate and thus it is not very suitable for midge development. It occurs at the same time of year, in a similar situation and in the same varieties as the Type I split, but much less frequently.

Type III split. This split is typical of the middle and late phases of growth of most varieties. Splitting first occurs at the base of the canes in mid-June and extends rapidly upwards in July and August, ceasing in September. The first splits are morphologically similar to Type I splits although pre-split areas do not occur, possibly because the outer layers have become tougher by this time. From mid-July onwards all the cortical parenchyma cells are involved in the splitting so that a clear separation occurs between them and the periderm. (Fig. 5(b).) The split tissue remains in closer contact with the underlying cells than in the Type I and, being thicker, tends to remain green longer and to be even more suitable for midge development. (Plates I and II.) It is probable that, as in many perennial plants, the development of a periderm layer is largely responsible for the splitting and shedding of the outer cortical layers. Although varieties differ in their degree of Type III splitting, all split to some extent and there is not the sharp difference from year to year shown by the Type I split. The total amount of splitting may be very extensive, so that nearly all the lower 20 to 30 cm. of the outer cortex peels away. Thus the Type III split appears as a regular feature of cane growth probably associated with periderm production.

Slug damage. During May, the canes are frequently injured by slugs (*Agriolimax reticulatus* Müll.) which rasp away the epidermis and most of the parenchyma. Usually they leave no flap of separated tissue as in Type I and Type III splits but, by breaking the epidermis, they sometimes expose a Type I pre-split area. In the absence of more suitable sites, slug damage may contain a large part of the Generation 1 population. Usually it is limited in extent and ceases in early June.

Mechanical damage. This is usually of limited extent although it may be due to many causes and can occur at any time of year. Unless in the pre-split condition the outer cortical tissues rarely separate and thus can harbour few larvae.

Oviposition.

Midges will lay eggs in any type of epidermal damage but in the field large larval colonies are found only in Type I or Type III splits. In insectary experiments two series of canes were prepared with artificial damage resembling the main types found under field conditions, but as far as possible comparable in overall size. Counts made after midges had been allowed to lay eggs, show that the Type I split was much preferred by the females (Table I). Many larvae developed in the Type I splits, few in the Type II and none elsewhere.

TABLE I.

*T. theobaldi. Oviposition in artificially damaged canes.
Average number of eggs per cane.*

Date.	No damage.	Type I split.	Type II split.	Punctures.	Broken spine.
12th July, 1946 ..	0	128	3	16	1
23rd August, 1946 ..	0	272	54	28	50

In the field the eggs of Generation 1 are laid mainly in Type I splits, if these are available. If slug and mechanical damage are present both usually receive a few eggs. Occasionally, single eggs or larvae may be found in small splits resembling Type I in petioles and in fruiting laterals, and Type II splits are also used to a small extent. In 1948 quite healthy larval colonies were found in the previous year's Type III splits on the fruiting canes of the variety Newburgh. In years when Type I splits are few, more eggs are laid in these other types of cover. If, before the end of Generation 1 oviposition, Type III splits begin to occur, most of the remaining eggs will be laid in them. Because it provides the only really favourable form of oviposition cover, the amount of Type I splitting is the dominant factor influencing the size of Generation 1.

Generations 2 and 3 use Type III splits almost exclusively. As the splits at the bottom of the cane dry up or are colonized by midge larvae, they cease to be attractive to the females, which then use the newer splits above. In susceptible varieties there are nearly always more Type III splits than are needed by these generations. The changing use of the four main types of oviposition cover throughout a summer season is shown graphically in Fig. 7, using data from the population count cane samples.

Larval feeding.

The larvae live in the outer cortical tissues from which they extract liquid nourishment, leaving the cell walls intact. The cells directly affected are the outer cortical parenchyma and/or the periderm. The overlying cells are also killed but, as they would die in any case, this damage is not important. The cells immediately below the larvae are the most severely affected; within a day or two they show

brown discoloration in patches which may grow to 10 sq. cm. or more in area but usually only two to three cells in depth. Although this damage is very superficial, it appears to be enough to throw the affected area of the cane open to attack by fungal parasites which can cause injury to the vascular tissues and cambium.

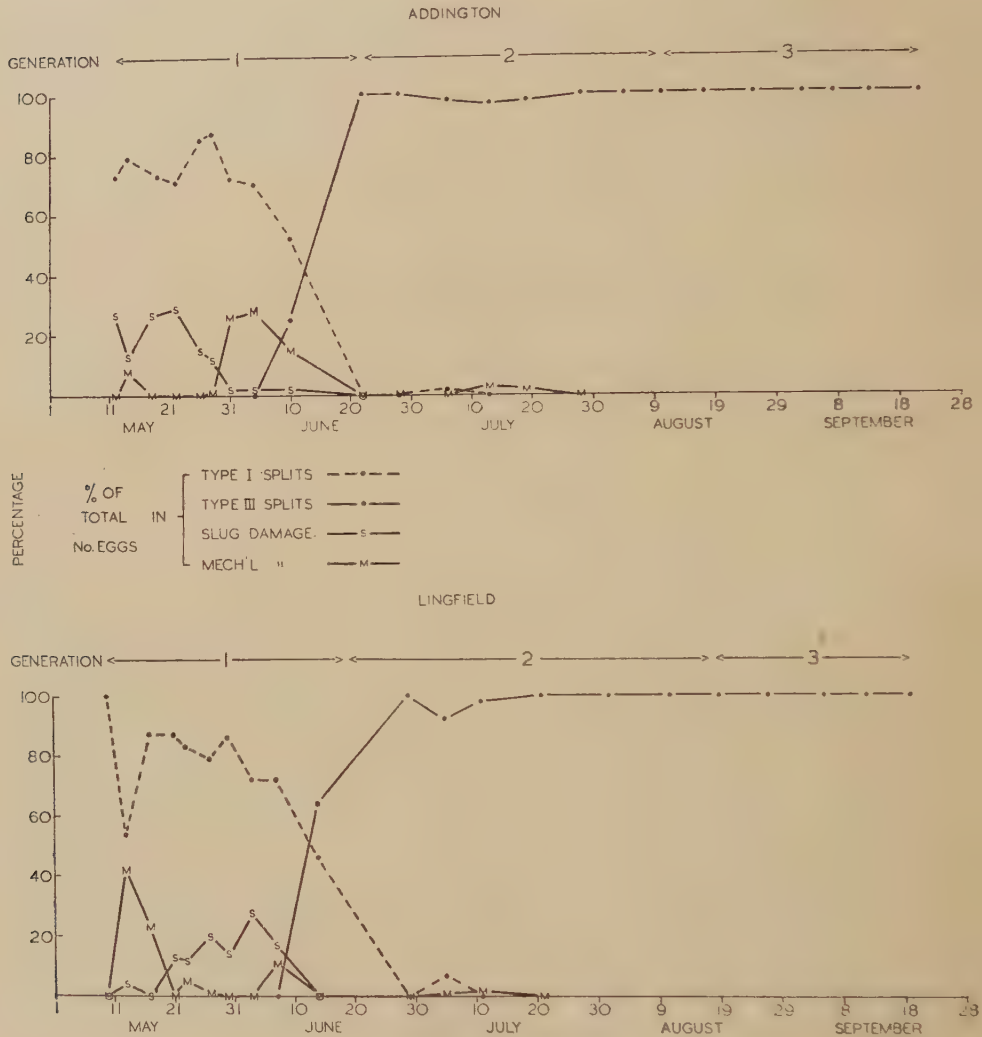


FIG. 7.
Oviposition sites, 1948.

Generation 1 larvae cause few lesions compared with those of later generations, but they damage the cane at a time when the tissues are soft and very vulnerable and thus the effect on the cells is more drastic. In Type I splits, the larvae feed on the outer cortical parenchyma. By the end of Instar I, four to five of the outer

cell layers are brown and partly collapsed, so that the larvae lie in small hollows of discoloured tissue. Instar II larvae extend the damage to the remaining parenchyma and to the few periderm cells which are now forming. At this stage (May, Fig. 5(a)), the periderm gives little or no protection, so that, by the time the larvae are fully fed, the browning may have penetrated to the cambium through the pericycle and phloem.

The lesions of Generation 2 are most commonly sited in the early Type III splits near the base of the canes. At this stage the periderm is about 8 cells thick, but still in active growth and relatively soft and green. The earliest larvae feed on the cortical parenchyma similarly to those of Generation 1, but the majority lie directly on the periderm. The parenchyma is affected quite quickly, but even Instar III larvae do not produce more than a superficial browning of the periderm. (July, Fig. 5(b)). Thus Generation 2 lesions are much more numerous but less deep than those of Generation 1, and may be present on nearly all the canes in susceptible varieties. The total surface area of cane damaged greatly exceeds that of the other generations put together and on individual canes it is often concentrated towards the base. Because of this the feeding of Generation 2 larvae opens the way to the most damaging fungal attacks of the season.

The lesions of Generation 3 vary in number from year to year, but in general they occur higher on the cane and are more scattered than those of Generation 2. All the larvae feed on the periderm which is now well-developed and approximately 15 cells thick. The larvae sometimes appear to have difficulty in extracting sufficient nourishment and the feeding period is often prolonged. The effects are much less marked than are those of Generation 2, browning of the periderm and of overlying cortical parenchyma being slow to develop.

A projection of the cane surface in the form of a map gives a clear picture of the extent and distribution of the damage. Two typical canes are shown thus in Fig. 8; the right-hand cane has suffered only a moderate attack, but even here the concentration of damage at the base, so typical of Generation 2, is well marked and would probably suffice to cripple or kill the cane.

Most of the above information was derived from an examination of the variety Newburgh, but in all essentials it holds good for other susceptible varieties.

Varietal susceptibility.

A characteristic feature of past records of *T. theobaldi* has been the restricted range of varieties suffering severe damage. All Theobald's early reports refer to the variety Bath's Perfection. Later, Reader's Perfection and Lloyd George were included but, when Bath's Perfection went out of common cultivation, reports of midge damage became much less frequent. With the introduction of the variety Newburgh, the midge came to the fore again and later caused severe damage to some of the new East Malling seedlings. At the other extreme, the widely grown Norfolk Giant is little affected. It has been shown above that, although the midge can breed in small numbers in damage caused to the cane by external agencies, the establishment of a large population depends on the provision of cover by the cane itself in the form of natural splitting. The amount of such splitting is a varietal characteristic that largely determines susceptibility to damage by midge.

In 1947 and 1948 a series of observations were made on Malling Enterprise and Landmark, which had proved respectively the most and the least susceptible

to midge damage in previous years. Preliminary work in the insectary showed that, given an equal amount of exposed tissue, midges laid approximately equal numbers of eggs on each variety. A series of 40 to 60 canes of each of the two varieties was chosen for closer field study. At weekly intervals the canes were examined and

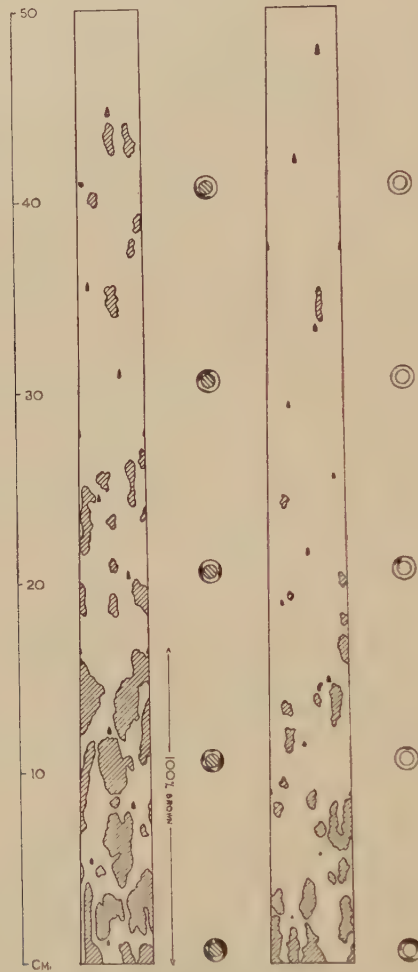


FIG. 8.

Map and cross-sections of damaged canes.

their height measured to indicate their growth rate. The position and amount of all epidermal damage was noted and classified under one of the following headings—(i) Type I splits, (ii) Type III splits, (iii) Slug damage, (iv) Mechanical damage. All midge lesions and any independent fungal lesions present were recorded and marked so that new damage could be readily seen. Type I splits, slug and mechanical injuries were counted and measured. Type III splits were too extensive for individual

attention and were recorded by measuring the height of the topmost split and assigning a category number from 0 to 5 indicating the degree of splitting present at the base of the cane. Thus it was possible to know at any time the total number of midge lesions that had occurred and the amount of cover available to the midge under each head on each variety. It was found that the area of Type III splits greatly exceeded that of any other form of cover. For a numerical comparison, a series of coefficients were calculated which estimated fairly accurately the relative amount of cover provided. (Table II.)

The Type I, slug and mechanical coefficients were calculated as follows, it being assumed that the correlation between the quantities in the numerator are much the same, whatever the variety and whatever the year :

$$\frac{\text{Average length of injury} \times \text{Average No. injuries per cane} \times \text{No. canes affected.}}{\text{Total No. canes.}}$$

The Type III coefficients were calculated as follows :

$$\frac{\text{Average maximum height of splits} \times \text{Average category} \times \text{No. of canes affected.}}{\text{Total No. canes.}}$$

TABLE II.

Relation of midge lesions to splitting and other damage in the varieties Malling Enterprise and Malling Landmark.

Coefficients.									Total Midge lesions.	
Type I.		Slug.		Mechanical.		Type III.				
	E.	L.	E.	L.	E.	L.	E.	L.	E.	L.
1947	0.13	0	0.08	0.02	0.47	0.36	346.4	96.7	950	274
1948	9.8	0	0.14	0	0.77	0.85	452.0	85.4	1,884	400

The Type III cover coefficient when plotted against time shows a remarkably close relationship to the occurrence of midge lesions in each variety. (Fig. 9.) The intensity of Type III splitting is clearly the major factor favourable to midge attack and subsequent fungal invasion. It thus has an important bearing on varietal susceptibility although there may be other factors, such as varying resistance to fungal invasion which affect the amount of cane death. The direct effect of the amount of Type I splitting on the season's total of lesions is small but, by its limitation of Generation 1, it has an important bearing on the size of the midge population in Generation 2. ^{see p. 85}

Thus a resistant variety escapes severe midge attack in two ways :

- (1) By providing no Type I splits, it allows only a small Generation 1 and thus limits the population for the whole year.
- (2) By providing very few Type III splits, it offers only a small vulnerable area to Generation 2. This is an effective defence even when exposed to a high population of midges, i.e. when growing next to a susceptible variety.

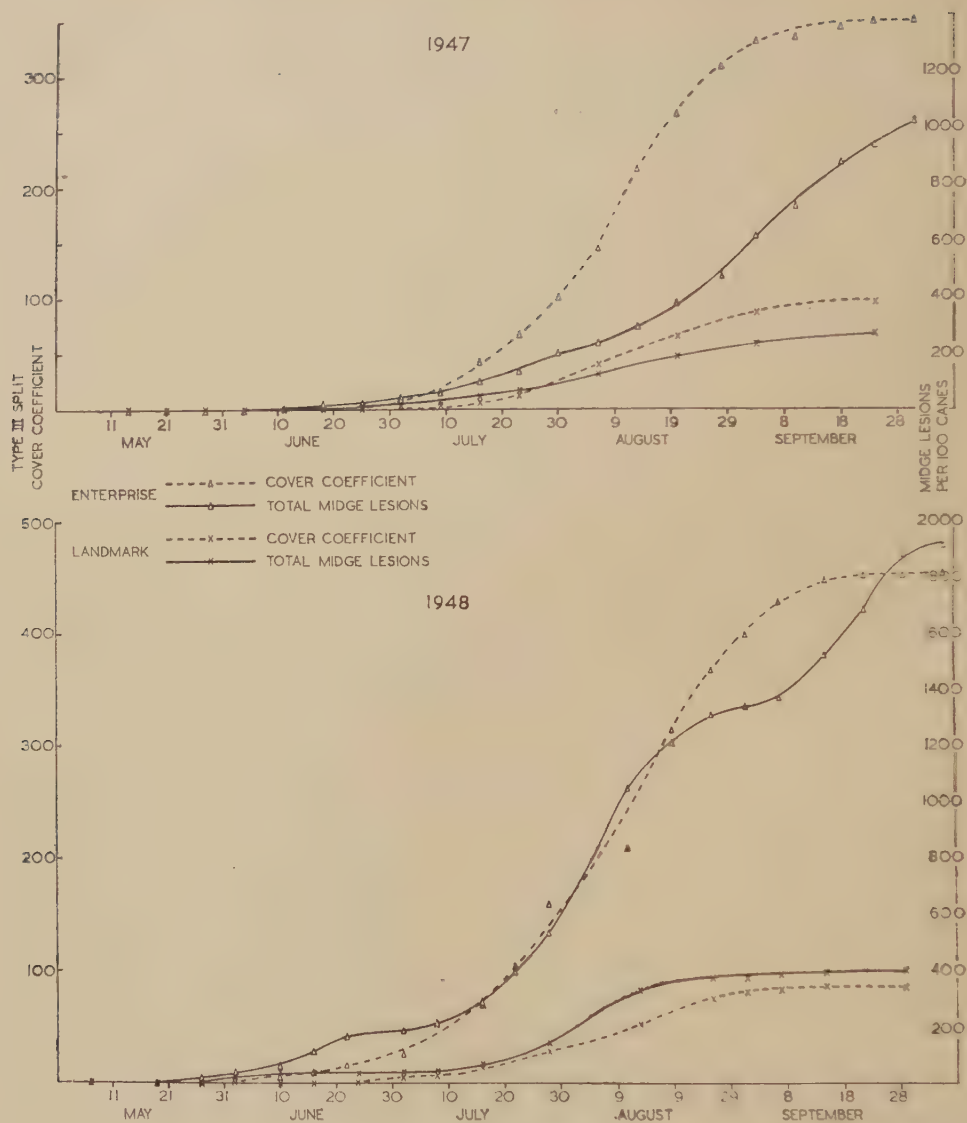


FIG. 9.

Relation of splitting to varietal susceptibility.

PARASITES AND PREDATORS.

Parasites.

Barnes (1944) reported that parasitized midge larvae remained on the cane throughout the winter. The parasite concerned has been identified, together with others which do not arrest the development of the host larva until after the cocoon has been formed. The latter group will be described first.

At least two species are involved, viz. *Piestopleura catillus* Walk. and *Leptacis* sp. (Scelionidae, Hymenoptera). They have been considered together in the following observations. In the spring the parasites emerge considerably later than the host (3rd June to 3rd July, 1947 and 1st to 22nd July, 1948) and attack principally the second generation of midge larvae. Imagines of the following generation emerge in late August and parasitize the third midge generation. Only once has the degree of parasitism noted been considerable, affecting 20 to 30 per cent. of the host larvae. Eggs are laid in midge larvae in their final instar while they are still on the cane. Parasitized larvae fall to the ground in the normal way but, after they have formed a cocoon, their skin becomes swollen and hard; and within this the parasite larva grows and pupates.

The parasite noted by Barnes is *Tetrastichus inunctus* Nees (Eulophidae, Hymenoptera). It has been found in small numbers in several localities and at Lingfield it increased markedly between 1946 and 1948 until in the latter year it caused a considerable reduction of the second and third midge generations. (Fig. 2.). Imagines emerge before the other parasite species (28th May to 3rd June, 1947), and attack mainly the first larval generation of the midge. The females locate the host larvae by use of their antennae and drive the ovipositor perpendicularly through the plant tissue to reach them. The midge larvae are soon immobilized and metamorphosis of the parasite takes place within their bloated and blackened skins. Emergence begins again in August, leading to parasitism of the late second and the third midge generations. The resulting larvae overwinter on the canes within the host skins, as reported by Barnes.

Predators.

Larvae of a predaceous gall midge (*Lestodiplosis* sp.) have already been recorded by Barnes (1944). They are to be found in the splits on the canes from mid-July onwards, but their effect is small as their numbers have never exceeded 2.6 per cent. of the midge population.

Nymphs of *Anthocoris nemorum* L. (Hemiptera) have been seen to feed on midge larvae, but they do not markedly reduce the population.

HOST PLANT RANGE.

The morphological differences within the genus *Thomasiniana* are so slight that they do not suffice to separate the species. Barnes, however, has shown that a study of the host plant range will show more positive distinctions between them.

He found (1931) that *T. oculiperda* would not oviposit on raspberry; (1939) that *T. crataegi* would not oviposit on raspberry or rose, and (1944) that *T. theobaldi* had a much wider range, ovipositing on raspberry, blackberry (wild, Himalaya Giant and Cut-leaf), loganberry, rose, apple, hawthorn, plum and quince, but not on cherry, currant (red and black), gooseberry or Worcesterberry. Larvae survived only on raspberry, Himalaya Giant blackberry, loganberry and rose. Further work along similar lines was undertaken in an attempt to clarify the position of the species *theobaldi*.

The following host plants were used. Raspberry (Malling Enterprise), wild and cultivated blackberry (Himalaya and Cut-leaf), loganberry, rose, apple (rootstock M.IX), hawthorn, blackthorn, plum (Myrobalan B), cherry (Mazzard F.12/1), quince (Malling C), pear and peach.

Wherever possible, material was taken from the same source for each experiment. At first, potted plants were used but these were later discarded in favour of cut shoots. The plant material was placed in an insect-proof compartment of an unheated insectary or in a large cage within the compartment. The host plants were slit so that each offered the same amount of cover for midge oviposition. Usually cuts 1 or 2 cm. long were made with a scalpel and the outer tissues raised on one side to provide a flap resembling natural splitting on the raspberry. This cover was readily used for oviposition and was suitable for development of larvae provided that the host plant also was suitable. Newly emerged midges were released in the compartment or cage so that they had an equal opportunity of visiting each of the host species.

Counts of eggs were made 2 to 3 days after first exposure, giving an estimate of the relative acceptability of each host to the midges, while counts of larvae (made 2 to 3 weeks later when most had reached Instar III) gave an estimate of their ability to feed and grow on each host. All the midge material used in these experiments was bred from larvae obtained from the field.

Experiments in 1946 were confined to observations on oviposition preferences and the growth of larvae on two series of pot plants in the insectary, supported by the sleeving of midges on growing plants in the field. The results obtained agreed closely with those of Barnes (1944) having in common the rather strange feature that midges would lay eggs readily on two hosts (*viz.* wild blackberry and apple) on which no larvae survived.

The 1947 experiments were designed to obtain some numerical comparisons of these and other points. Two oviposition experiments were carried out on cut shoots and two larval survival experiments on potted plants. In Trial 3 (see Table III) the number of attacked slits was noted in place of a larval count. All figures are expressed as a percentage of the raspberry figures, which are given in the first column. (Table III.) The results resembled those of 1946. In 1948 a technique capable of statistical analysis was adopted. Seven replicates of each host plant were used, arranged in a random order. The shoots were retained for larval counts at a later date, giving the results expressed in Table IV.

The results of statistical analysis are set out below. Host plants showing no significant difference are bracketed together. Because of the large number of zero counts the main analysis of variance excluded cherry, quince and plum, which were compared with each of the others by a randomization test. The variable results given by rose often made the difference with plum non-significant, but little importance need be attached to this.

Eggs: Trial 1.

Cherry, Quince, Plum, Hawthorn, Blackthorn, Apple, Rose, Wild Blackberry,
Raspberry, Loganberry.

In addition, rose and plum showed no significant difference.

Eggs: Trial 2.

Blackthorn, Plum, Hawthorn, Apple, Wild Blackberry, Rose, Cut-leaf Him. Giant
Loganberry, Raspberry.

TABLE III.

T. theobaldi host plant preference trials, 1947.*Eggs laid and larvae developing on various host plants, expressed as a percentage of the total numbers recorded on raspberry.*

Trial No.	Date.	Raspberry.		Logan-berry.	Wild black-berry.	Rose.	Appel.	Haw-thorn.	Plum.	Cherry F5/4.	Pear.	Peach.
		No.	%									
1	11th August	574	(100)	104	98	77	8	3	Czar 46	0	2	10
2	23rd August	847	(100)	156	49	80	22	1	Victoria 3	0	18	—
3	30th May	—	(100)	82	LARVAE.		0	0	—	—	—	—
4	21st August	190	(100)	35	0	33	0	0	—	—	—	—

TABLE IV.

T. theobaldi host plant preference trials, 1948.

Eggs laid and larvae developing on various host plants, expressed as a percentage of the total numbers recorded on raspberry.

Trial No.	Date.	Raspberry.		Loganberry.	Blackberry.			Rose.	Apple.	Hawthorn.	Blackthorn.	Plum.	Cherry.	Quince.
		No.	%		Wild.	Cut-leaf.	Himalaya Giant.							
1	2nd Sept.	781	(100)	106	.46	—	—	25	14	1	5	0.4	0	0
2	12th Sept.	776	(100)	79	25	34	39	28	9	2	0	0.9	—	—
								LARVAE.						
1	21st Sept.	290	(100)	114	2*	—	—	36	0	0	5*	0.7*	0	0
2	29th Sept.	606	(100)	68	0	0.3*	34	25	0	0	0	0.5*	—	—

* Small larvae which failed to mature.

Larvae : Trial 1.

Apple,	Hawthorn,	Cherry,	Quince,	Wild Blackberry,	Blackthorn,	Plum,	Rose,
							
Raspberry, Loganberry.							

Larvae : Trial 2.

Wild Blackberry,	Apple,	Hawthorn,	Blackthorn,	Cut-leaf Blackberry,	Plum,	Rose,	Him. Giant Blackberry,
							
Loganberry, Raspberry.							

The three years' results may be summarised as follows :

(1) Raspberry and loganberry are preferred for oviposition and are more suitable for larval development than any other hosts offered. In the field, loganberry splits but little and is rarely attacked.

(2) Himalaya Giant blackberry and rose are possible host plants, but they do not split freely and cannot support large populations in the field.

(3) Wild and Cut-leaf blackberries, although well favoured for oviposition, fail to nourish the larvae.

(4) Apple receives about one-tenth of the number of eggs laid on raspberry, but no larvae survive to maturity.

(5) The other plants receive very few eggs, from which no larvae survive, and may be considered as species on which oviposition is most unlikely to occur in the field.

It is therefore concluded that *T. theobaldi* is a distinct species which is incapable of reaching large numbers in the field on any host except the raspberry. Its interrelation with the other species of the genus will form the subject of a later publication.

SUMMARY.

An account is given of the biology of the Raspberry Cane Midge (*Thomasiniana theobaldi* Barnes) including notes on distribution and external morphology.

In the field, three generations usually occur in the course of a year. Eggs are laid under the broken epidermis of the raspberry cane, giving rise to colonies of pink larvae, the feeding of which causes damage to the outer cortical tissues. Pupation occurs in a cocoon in the surface soil at the base of the cane.

The growth of the raspberry is often accompanied by a natural splitting of the epidermis and outer cortical tissues of the cane which provides a suitable shelter for the eggs and larvae. The amount of such splitting is often the most important factor affecting varietal susceptibility to midge damage.

Three hymenopterous parasites have been recorded, one of which may appreciably reduce the size of the later generations. Two predators of minor importance are also described.

Host plant preference trials confirm *T. theobaldi* as a distinct species.

ACKNOWLEDGMENTS.

This entomological investigation (see also Part II) has been directed by Dr. A. M. Massee in close contact with the Plant Pathology Section headed by Dr. R. V. Harris. Mr. N. H. Grubb has given pomological advice. Miss Eleanor C. Thompson has prepared the photomicrograph and Mr. E. Y. Jones the photographs. Miss Margery Bennett and Miss Joan R. Groves have given assistance with the field records.

The author also acknowledges the help of Dr. H. F. Barnes of Rothamsted, whose continued interest has been of especial value and that of the late Mr. G. Fox Wilson and Messrs. D. E. Green and J. M. S. Potter of the Royal Horticultural Society. Mr. G. E. J. Nixon of the Commonwealth Institute of Entomology and Dr. C. Ferrière of the Muséum d'Histoire Naturelle de Genève, have kindly identified the Hymenopterous parasites.

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PLATE I.



FIG. 3.
Early stage midge lesion in Type III split. ($\times 1\frac{1}{2}$).

PLATE II.



FIG. 4.
Late stage midge lesion in Type III split ($\times 1\frac{1}{2}$).

PLATE III.

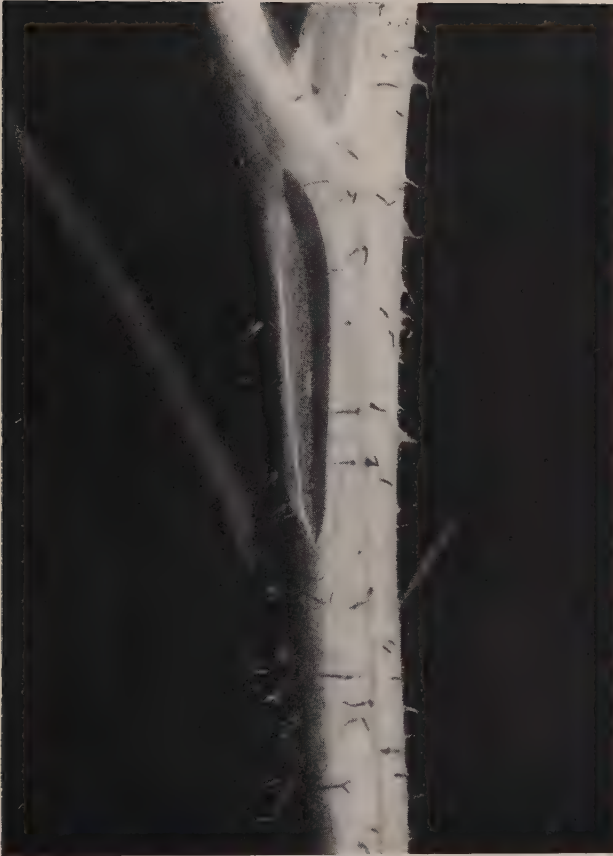


FIG. 6.
Newly formed Type I split ($\times 2$).

OBSERVATIONS ON THE RASPBERRY CANE MIDGE (*THOMASINIANA THEOBALDI* BARNES)

II. "MIDGE BLIGHT", A FUNGAL INVASION OF THE RASPBERRY CANE FOLLOWING INJURY BY *T. THEOBALDI*

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KNOWN associations between insects and plant pathogens range from symbiosis through the vector relationships to the simpler cases in which insect damage to the epidermis admits wound parasites to the plant tissues. The present case differs in one important respect from the latter, namely, that the epidermis is already ruptured before the insect damage begins. Published work on the association of gall midges with fungi mostly refers to the specialized cases of the "Pilzgallen" or ambrosia galls in which the larvae appear to live in symbiosis with fungi which grow within their galls, e.g. Neger (1908). Koronèos (1939) and Silvestri (1949) refer to fungal damage to olives following oviposition by a midge, but here the situation is complicated by the presence of the fly *Dacus oleae* Rossi which makes the initial puncture in the fruit.

The results of studies on the part played by *T. theobaldi* in the fungal invasion of raspberry canes have already been briefly described (Pitcher and Webb, 1949). The present more detailed account, which should be read in conjunction with Part I of this series (p. 71), falls into the following sections:

1. Observations showing that fungal invasion does, in fact, follow midge injury to the canes.
2. The fungal pathogens involved and the means by which they are enabled to invade the cane.
3. An account of the nature and extent of the damage promoted by each larval generation of the midge.

THE SEQUENCE OF ATTACK.

The simplest example is provided by the second larval generation. It has been shown (Part I, p. 85) that the most severe damage visible by the time that the larvae are ready to leave the canes in late July is a superficial browning of patches of periderm to a depth of 2 to 3 cells only. Two to three weeks later these lesions appear as dark areas, slightly sunken below the level of the surrounding periderm. After mid-August fungal fructifications develop within these sunken areas but *not* on the surrounding undamaged periderm (Figs. 1-3). Transverse sections show that the discoloration is no longer superficial but is penetrating between the pericycle

* The entomological data contributed by this author form part of a thesis approved for the Degree of Doctor of Philosophy in the University of London.

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fibre bundles into the vascular tissues (Fig. 5(b), Part I). By October, discoloration has reached the pith, first passing through the xylem down the medullary rays and thus affecting the whole sector lying below the midge lesion (Fig. 4). The extremely local nature of this damage makes it clear that the fungi have entered the cane where its surface has been modified by the feeding of the midge larvae and have penetrated radially from this point. Tissues exposed by splitting but not attacked by the midge are not subject to fungal attack and continue to grow normally.

In the examination of marked canes described in Part I (p. 86), the precise origin of each fungal lesion was known from the weekly inspections of the canes and it was found that nearly all were preceded by midge attack. A small amount of independent fungal invasion of the canes did occur, but the lesions were quite distinct from those following midge injury. They were for the most part due to *Didymella applanata* and *Botrytis cinerea* and damaged the cortical parenchyma only. In 1947 and 1948 they did not exceed 4 per cent. of the total midge lesions suffered by the susceptible variety Mallings Enterprise.

The situation following damage by Generation 1 is not quite as clearly defined, as vascular injury occurs while the larvae are still on the cane. Fungal attack proceeds more quickly in the tender tissue and possibly overtakes the midge injury. Occasionally fructifications can be found on the older parts of the lesion before all the larvae have left. Fungal attack following Generation 3 is less severe and sometimes does not occur at all.

There are thus three main stages in the sequence of events :

- (1) The outer cortical tissues of the cane split.
- (2) The midge larvae feed on the tissues exposed by the split.
- (3) Fungi become established on the cells damaged by the midge and later penetrate to the underlying vascular tissues.

Fungal invasion cannot follow stage (1) without the interpolation of stage (2), because natural splitting forms a unique type of wound which is not susceptible to fungal attack, although acceptable to the midge. Thus the midge appears quite clearly as the precursor of the fungal damage which often leads to the death of the cane.

THE FUNGI INVOLVED.

Three fungi that have been isolated consistently from lesions within the feeding areas of midge larvae have proved capable of producing similar lesions when re-inoculated into young canes. Two of them, *Leptosphaeria coniothyrium* (Fckl.) Sacc. and *Didymella applanata* (Niessl) Sacc. have been recorded previously as parasites of *Rubus* species. The third, *Fusarium culmorum* (W. G. Smith) Sacc., is a well known pathogen of cereals but has not, as far as is known, been recorded on *Rubus* species prior to this investigation.

The relative frequency of the pathogens varied considerably in different years and in different localities. *L. coniothyrium* was usually the least common but where it did occur it caused rather more serious damage than did either of the other two fungi. *F. culmorum* predominated on the American variety Newburgh, but none of the other raspberry varieties on which observations were made showed a marked susceptibility to any one pathogen. These included Norfolk Giant, Lloyd George, Hercules, Park Lane, Chatham, and the range of Mallings Seedlings.

L. coniothyrium has been recorded on raspberry in North America by Anderson

(1920) and Bennett (1930) and in this country as the cause of "Cane Blight" of raspberry by Harris (1931) and Wormald (1935). Cane Blight disease is at present often confused with the death of fruiting canes which follows midge injury to first year canes. To distinguish between them it is proposed to refer to the latter as "Midge Blight". The superficial symptoms of these two diseases differ as follows: Midge Blight lesions are centred in the midge larval feeding areas which are sunken as previously described and, although concentrated towards the base of the cane, they may occur up to 60 cm. above soil level (Fig. 8, Part I). The majority of Cane Blight lesions occur at or just below soil level. They may also occur at any place mechanically damaged, e.g. by wind-rubbing on the wire work. No part of the lesion shows the smooth shallow depression which is characteristic of Midge Blight. In both diseases the fungus causes a dark patch on the bark and later produces pycnidia (Fig. 1) containing small dark spores. *L. coniothyrium* is pathogenic to several members of the Rosaceae and has produced pycnosporos in culture on damp straw, on strawy horse manure and on spent hops, all of which materials may be used as a mulch for raspberry canes.

Didymella applanata has long been recognized as the cause of the superficial "Spur Blight" disease of raspberries; the first record of it was on material collected in England by Niessl (1875). There is, however, a marked difference between the symptoms of Spur Blight and Midge Blight even though the same fungus is involved. In Spur Blight, as pointed out by Koch (1931), the mycelium is confined to the outer cortex because it is apparently unable to penetrate the undamaged periderm. The lesion caused by *D. applanata* on larval feeding areas (Fig. 2) is much deeper, frequently penetrating to the pith and killing the cane as is the result with the other two pathogens. The apparent failure of *D. applanata* to penetrate the undamaged periderm was confirmed by comparing the progress of artificial inoculations made by the following methods.

- (a) By rubbing the bark with a pycnospore suspension containing carborundum powder.
- (b) By placing mycelium on a light surface abrasion made with a scalpel.
- (c) By inoculating a deep scalpel cut with either (i) a pycnospore suspension or (ii) mycelium.

Ten canes were inoculated by each method, the wound being covered with "Cellophane" for seven days to prevent the entry of unwanted organisms. Spore suspensions were not washed and culture medium was not removed from mycelium. Methods (a) and (b) produced nineteen "Spur Blight" type lesions, the hyphae remaining in the outer cortex and causing little damage to the cane. One inoculation (b) with mycelium failed completely. The twenty deep inoculations all produced serious lesions, eleven of the canes subsequently dying. The damage caused by midge larvae is thus comparable in effect with the deep inoculation.

Pycnidia of *D. applanata* and *L. coniothyrium* were both seen on young canes in the field in summer, and persisted until September in the following season, during which time viable spores were always obtainable from them. Perithecia were comparatively uncommon and were found mainly in spring.

Fusarium culmorum is easily recognized on the cane by its pink sporodochia (Fig. 3) and it is the first of the three fungi to fruit in the field. This is possibly because spores can be produced more rapidly than they can with the other two pathogens, both of which take at least four weeks to spore in culture as compared

with 5 to 8 days for *F. culmorum*. Unlike *Didymella* and *Leptosphaeria* this fungus was not seen on the young canes after September.

Many fungi other than these three were isolated from fruiting bodies in canes but only two regularly produced lesions when re-inoculated. These were *Coryneopsis rubi* Grove and *Camarosporium rubicolum* Sacc. Both produced mild lesions without serious damage to the cane.

The rapid succession of larval infestation and fungal infection suggests the following two possibilities :

- (i) The midge carries spores of pathogenic fungi to the cane during oviposition.
- (ii) There are sufficient spores of the pathogenic fungi already present on the surface of the cane in the field to account for the frequent infection of larval feeding areas.

The possibilities were investigated as follows :

- (i) Soon after their emergence from field soil in the laboratory, adult midges were allowed to fly in petri dishes containing 2 per cent. malt agar. Colonies which developed were all of a species of *Cunninghamella*, with which the soil was heavily contaminated. A second similar investigation resulted in the appearance of 94 colonies of *Penicillium* species and one colony of a yellow *Fusarium* sp. Midge adults caught in the field gave rise to various fungal colonies, but never to one of any of the three pathogens.
- (ii) A survey of the fungus flora of the cane was made at the heights of 5 in., 10 in., and 15 in. from the soil. Pieces of bark 5 mm. square were removed, placed surface downwards on 2 per cent. malt agar plates and "streaked". Developing colonies were removed to slopes of 2 per cent. malt agar as they appeared. The results of these observations are tabulated below :

Numbers of fungal colonies from 10 canes of "Malling Enterprise".

Fungus.	Height above soil level		
	5 in.	10 in.	15 in.
Non-pathogenic ..	182	161	143
<i>L. coniothyrium</i> ..	14	10	9
<i>D. applanata</i> ..	3	8	11
<i>F. culmorum</i> ..	24	15	8

These numbers give a mean of at least one spore of each of the pathogens per square cm. of cane surface and, taking into account the re-distribution of spores by rain, this is considered sufficient to account for the high frequency of infection of larval feeding areas.

Midge larvae do not move about the cane, and are not therefore suspected of carrying spores. Their oesophagus is too small to admit a spore of 2 μ diameter, which is the smallest produced by the pathogens. Numerous bacteria were seen in the gut, however, and when larvae were allowed to move over agar plates a continuous trail of bacterial colonies appeared within 48 hours. These bacteria were examined for cellulase and pectinase enzymes, and one type, not identified, was shown to possess a cellulase but no activity was shown against apple pectin in a solution containing both glucose and pectin in a pH range of 4 to 7.5. It is possible

therefore that the cellulase enzyme activity of the bacteria may add to the damage caused to the cane by the larvae.

Thus the midge appears not as a vector of the fungal pathogens but as the producer of a substrate on which spores already present on the cane can germinate and invade the underlying tissues.

ULTIMATE EFFECT ON THE RASPBERRY CANE.

As the season progresses, the gradual maturation of the first-year canes increases their resistance to midge and fungal injury. For this reason each midge generation promotes a distinct and characteristic type of injury.

Generation 1.

All growth in the affected area ceases at an early stage but the surrounding tissue continues to thicken normally, so that a hollow, resembling a canker, is produced (Fig. 5(a), Part I). If this is of moderate size, the growth of the cane is little affected and a normal crop may be borne in the following spring. Canes bearing large cankers are mechanically weak and are easily snapped, e.g. by gales.

Generation 2.

The symptoms of the gradual radial penetration of the fungi have been described above. Soon after the midge larvae have left the cane, all growth of periderm ceases in the affected area but, around this, the undamaged periderm continues to thicken normally, leaving the midge lesion as a typical irregularly-shaped sunken area. Further development of vascular tissue ceases when the cambium is reached but, because the cane is more mature, no canker is produced although there may be a slight flattening of the cane in the earlier lesions. A few weeks later, the discoloration spreads along the medullary rays to the pith until a sector of xylem is discoloured (Fig. 5(b), Part I). These effects are normally confined to tissue within the limits of the surface sunken area but, if the cane becomes moribund, secondary browning may extend to the whole of the basal area (Fig. 8, Part I). Although the lesions of Generation 2 are individually less severe than those of Generation 1 they are more numerous and tend to be concentrated at the base of the cane so that their cumulative effect is much greater. For this reason Generation 2 is responsible for most of the dead canes and also for many in which vigour and fruit yield are reduced.

Generation 3.

The earlier and more severe lesions may produce sunken areas followed by the death of patches of vascular tissue as in Generation 2. In many cases, however, the mature periderm receives only superficial injury and continues to give complete protection to the vascular system.

SUMMARY.

Larvae of the Raspberry Cane Midge (*Thomasiniana theobaldi* Barnes) are known to cause superficial damage to first-year raspberry canes. Tissue damaged by their feeding is frequently invaded by fungal pathogens which may cause the death of the cane before it can bear fruit in the following season. This disease is given the name of "Midge Blight". The fungi principally involved are *Fusarium*

culmorum (W. G. Smith) Sacc., *Didymella applanata* (Niessl) Sacc. and *Leptosphaeria coniothyrium* (Fckl.) Sacc. Spores of all three species were found amongst the fungal flora of the epidermis of healthy canes but none could be cultured from the exterior of adult cane midges. It is concluded therefore that the midge larvae produce a substrate suitable for the development of spores of the pathogens which are already present on the canes. A brief account is given of the type of injury characteristic of each of the three larval generations of the midge.

ACKNOWLEDGMENTS

In addition to those mentioned in Part I, the second author wishes to thank Dr. R. V. Harris for his help and constructive criticism and for access to his unpublished records and observations. He is also indebted to Dr. W. L. Gordon, of Winnipeg, for the identification of *Fusarium culmorum*.

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PLATE I.

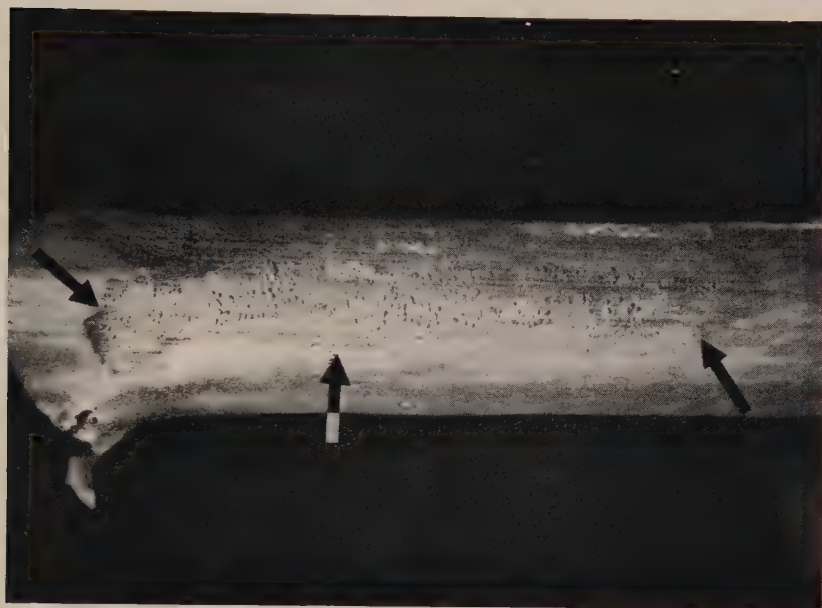


FIG. 2.
Didymella applanata on midge lesion ($\times 1\frac{1}{2}$).



FIG. 1.
Leptosphaeria coniothyrium on midge lesion ($\times 2$).

In all figures, the arrows indicate the margin of the midge lesions,

PLATE II.

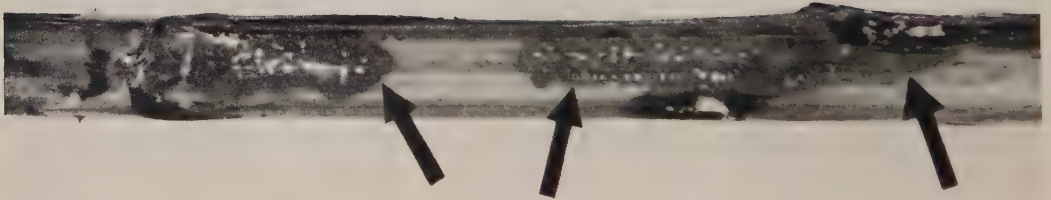


FIG. 3.
Fusarium culmorum on midge lesion (actual size).

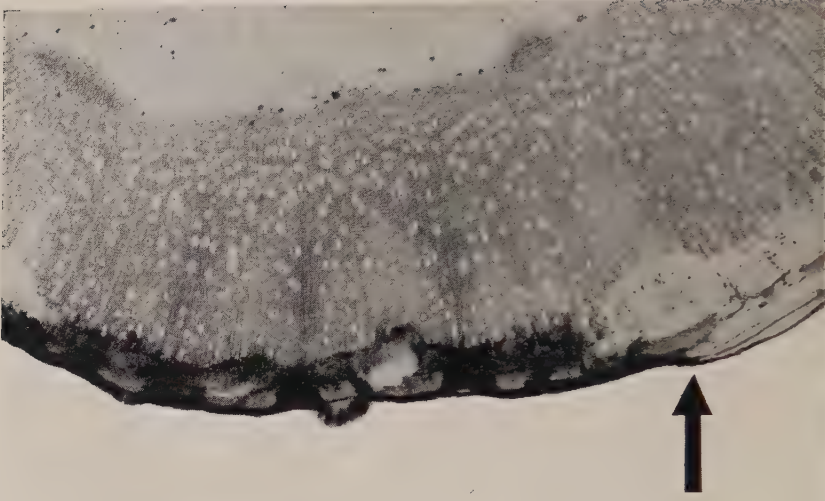


FIG. 4.
Transverse section of Generation 2 midge lesion invaded by
Fusarium culmorum. On Newburgh raspberry cane ($\times 24$).
See note below Figs 1 and 2.

SPACING EXPERIMENTS ON VEGETABLES

V. THE EFFECT OF SPACING AND MANURING ON THE COMPOSITION OF THE FOLIAGE OF SHALLOTS AND GLOBE BEET, CONSIDERED IN RELATION TO THE GROWTH OF THE PLANTS

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In two earlier papers (Warne, 1951a and b), yield data from two complex manuring and spacing experiments on shallots and globe beet were reported. These papers, however, left unanswered the question, "Why does close spacing restrict the size of the plants?" although it was suggested that competition for water and nutrients had been important with the shallots, and for nutrients and light with the beet. In this paper, chemical data will be presented which indicate the relative importance of competition for nutrients in restricting the growth of the closely spaced plants.

EXPERIMENTAL PROCEDURE AND RESULTS.

The procedure followed in the cultivation of the crops and in the assessment of yield has already been described (Warne, *loc. cit.*). Shallots of two sizes were planted on a fertile loam at two manurial levels (no manure and 10 cwt. per acre of a mixture of 3 parts of superphosphate of lime, 2 parts of sulphate of ammonia and 1 part of sulphate of potash) at all combinations of 3 row distances (8 in., 12 in. and 16 in.) and four planting distances (3 in., 6 in., 9 in. and 12 in.).

Beet were grown at two manurial levels (as for shallots) at all combinations of 4 row distances (9 in., 12 in., 18 in. and 24 in.), and three nominal thinning distances (2 in., 4 in. and 6 in.). These three thinning distances resulted in plant populations equivalent to 4.43, 2.88 and 2.18 plants per foot of row. The manuring caused a slight increase in the stand of beet plants but the main effect of manuring on yield was due to its influence on the growth of the plants.

PLANT GROWTH.

This has already been discussed (Warne, *loc. cit.*) in the form of yield per unit area but, in considering how the factors constituting the environment affect growth, it is the size of the individual plant which is of interest.

(a) *Shallots*. In the shallot the individual daughter bulb rather than the whole plant is probably the "competing unit", the growth of which is related to the amount and efficiency of the leaves at the bases of which it is produced. Consequently the yield data have been transformed into "weight per 100 daughter bulbs" with results that are assembled in Table I. The interpretation of these results is rendered the more difficult by the fact that the spacing, manuring and the size of the planting material affect the number of daughter bulbs produced per plant, so that the mean bulb weight is not an exact reflection of total yield. This spacing effect, however,

is small in relation to the effect of spacing on daughter bulb size. Reference to Table I shows that bulb size is affected greatly by the size of the planting material and by the spacing but only slightly by manuring.

(b) *Globe Beet*. The unit of growth chosen here was root weight. The Root/Top ratio was affected by the spacing and the manuring but this effect was slight by comparison with the effects on root weight which was highly positively correlated

TABLE I.
Growth data for Shallots. Weight (oz.) per 100 daughter bulbs.

Manurial treatment.	Planting material.	Row distance.	Planting distance				Mean.
			3 in.	6 in.	9 in.	12 in.	
No manure	Large	8 in.	15	30	44	54	36
		12 in.	24	41	53	59	44
		16 in.	35	51	57	87	57
		Mean	25	40	51	67	46
No manure	Small	8 in.	43	68	61	82	63
		12 in.	49	86	97	105	84
		16 in.	71	94	100	137	100
		Mean	54	83	86	108	83
Manure	Large	8 in.	23	31	58	51	41
		12 in.	36	50	69	70	56
		16 in.	34	52	74	66	57
		Mean	31	44	67	62	51
Manure	Small	8 in.	41	66	81	97	71
		12 in.	54	76	97	107	84
		16 in.	68	79	108	123	95
		Mean	54	74	95	109	84
Mean values							
No manure	—		39	61	69	87	64
Manure	—		43	59	81	86	68
—	Large		28	42	59	65	49
—	Small		54	79	90	109	84

with total plant weight. Reference to Table II shows that spacing and manuring both exert an appreciable effect on root weight.

Manuring affected the stand of plants and hence the mean area available per plant, but this effect was very slight by comparison with the effect of changes in the row and thinning distance on the available areas.

CHEMICAL COMPOSITION OF THE PLANTS.

For purposes of chemical analysis, leaves were collected from each plot. Leaves were chosen for analysis on the grounds both of convenience and suitability. The grounds for believing that the composition of the foliage is a reflection of the nutrient

TABLE II.

Growth data for Beet. Mean weight of roots in oz.

NOT MANURED. Row distance.	Thinning Distance.			Mean.
	2 in.	4 in.	6 in.	
9 in.	2.98	4.56	5.57	4.37
12 in.	3.17	5.10	6.88	5.05
18 in.	5.18	6.84	8.52	6.85
24 in.	5.15	8.17	9.93	7.75
Mean.	4.12	6.17	7.72	6.00
MANURED. Row distance.	Thinning Distance.			Mean.
	2 in.	4 in.	6 in.	
9 in.	3.23	4.36	5.94	4.51
12 in.	3.53	6.05	6.04	5.21
18 in.	5.41	7.26	8.89	7.19
24 in.	5.94	8.22	8.99	7.72
Mean.	4.53	6.47	7.46	6.15

status of the plant have been discussed by Goodall and Gregory (1947) and need not be restated here. The shallots were sampled on two dates in June and the beet in mid-August. At sampling, fully developed leaves not showing any signs of senescence were gathered and the whole shallot leaves and the laminae of the beet leaves were dried for subsequent estimation of phosphate, potash, calcium and total nitrogen.

(A) *Shallots.*

The chemical data for the two sampling dates are essentially alike, and only those of the second sampling will be discussed.

(i) *Manurial effects.* The effects of manuring on the composition of the leaves are summarized in Table III and it is seen that the manurial treatment significantly

TABLE III.

Composition of shallot foliage from manured and unmanured plots and from plants derived from "large" and "small" planting material.

Treatment	N ₂	K ₂ O	CaO	P ₂ O ₅
	as per cent. of dry weight.			
Manured	3.62*	3.37*	3.67*	0.77*
Unmanured	3.02	2.64	3.17	0.91
Large } planting material ..	3.22*	2.83*	3.50	0.88*
Small }	3.42	3.17	3.34	0.81

* Difference significant at $P=0.05$.

increased the contents of nitrogen, potash and lime, but decreased the phosphate content of the leaves. The increased contents of nitrogen and potash, following manuring, are in accordance with expectation, whilst the decrease in the phosphate content may indicate that the fertilizer mixture used was deficient in phosphate relative to its content of nitrogen and potash; but the result might be the same if the soil were originally high in phosphate, so that the additional phosphate in the manurial application was not needed by the plants. Alternatively, if phosphate uptake is restricted to a short period early in the growth of the plant, before any visible manurial response occurs (Warne, 1951a, p. 294) then a growth response to manuring occurring subsequent to a cessation or even slowing down of phosphate uptake might result in a decreased concentration of phosphate in the manured plants.

(ii) "*Size of planting material*" effects. Reference to Table III shows that a reduction in the size of planting material, which reduces the intensity of the competition by reducing the number of daughter bulbs produced per plant, has an effect on leaf composition similar to but smaller than that of manuring, increasing the contents of nitrogen and potash and decreasing the phosphate content. There is equally good agreement between the effects of manuring and of planting small material if, instead of considering the contents of nutrients in the leaves, the ratios, particularly of phosphate to other nutrients, are compared.

(iii) *Spacing effects*. In assessing the significance of row and planting distance effects the interaction of these two treatments was included in the estimate of error but the spacing effects were analysed separately for the four combinations of manuring and size of planting material. ("Large, manured", "large, unmanured", "small, manured", "small, unmanured").

(a) *Phosphate*. No significant effects of spacing were found.

(b) *Potash*. No significant effect was found, except for the row distance effect on the "large, manured" plots. The values for the 8 in., 12 in. and 16 in. rows were 2.5, 3.7 and 3.3 per cent., the value for the 8 in. rows being significantly lower than those for the other two row distances. Planting distance effects, although not reaching a significant level, were similar in their trend to those of row distance.

(c) *Lime*. A planting distance effect, significant on the "large" and nearly so on the "small" manured plots was found, the values obtained being shown below.

TABLE IV.

Showing lime (CaO) as percentage of dry weight of shallot leaves at various planting distances.

Treatment.	Planting distance			
	3 in.	6 in.	9 in.	12 in.
Manured, large planting material	3.29	3.62	3.81	4.03
Manured, small planting material	3.30	3.32	3.81	4.13

(d) *Nitrogen*. Significant row and plant spacing effects were found for all the "no manure" treatments (large and small planting material) and for planting

distances on the "manured, large" plots. The relevant data are summarised below.

TABLE V.

Showing contents of total nitrogen as percentage of dry weight in shallot leaves grown at several spacings.

Treatment.		Row distance			
Manurial.	Size of planting material.	8 in.	12 in.	16 in.	
No manure	Large	2.74*	2.89	3.11	
Manure	Large	3.39	3.38	3.61	
No manure	Small	3.00*	3.10	3.28	
Manure	Small	3.65	3.74	3.72	
		Planting distance.			
		3 in.	6 in.	9 in.	12 in.
No manure	Large	2.72*	2.85	3.07	3.02
Manure	Large	3.24*	3.65	3.63	3.59
No manure	Small	2.93*	3.01	3.30	3.26
Manure	Small	3.62	3.81	3.85	3.54

* Spacing effects significant at $P=0.05$.

Generally, where the spacing effects are significant, it is seen that wide spacing has an effect on composition similar to that of manuring or of reducing the size of the planting material, which by reducing the number of daughter bulbs produced per unit area reduces the number of competing units. These data suggest therefore that wide spacing, and the planting of small bulbs, both of which reduce competition, ensure an adequate supply of nutrients to the developing daughter bulbs just as manuring does and appears to lend support to the view that competition for nutrients is an important factor in restricting the growth of the closely spaced plants. Some of the observed effects are not susceptible of any simple explanation. Thus manuring, and wide spacing on the manured plots increase the content of lime in the leaves. This may be the result of the immobility of calcium in the leaf in which case the calcium content may give a rough measure of the rapidity with which the transpiration stream carrying nutrients has entered the leaf. During drought the widely spaced plants, and after drought the manured plants as well (Warne, 1951a, p. 294) were noticeably greener and perhaps transpiring more vigorously than the others.

The nitrogen data are of most interest. Manuring, decreasing the size of the planting material and wide spacing (generally) all increase the content of nitrogen in the leaves. Further, the factors which increase the nitrogen content of the leaves all increase bulb size, so that qualitatively it appears that close spacing, the planting

of large bulbs, and absence of manuring all restrict daughter bulb size by restricting the supply of nutrients and especially of nitrogen. When the results are examined quantitatively the agreement is not so good. Whereas manuring affects the composition considerably it alters bulb size only slightly, whilst spacing which affects the composition of the leaves less markedly has a large effect on daughter bulb size. The relation between bulb size and leaf composition has been expressed by calculating correlation coefficients (r) and the values obtained for r are assembled in Table VI.

TABLE VI.

Correlations between daughter bulb weight and contents in the leaf of shallots.

Treatments..	P ₂ O ₅	K ₂ O	CaO	N
All treatments	-0.30*	+0.46†	+0.06	+0.42†
All treatments involving large planting material	-0.05	+0.44*	+0.14	+0.55†
All treatments involving small planting material	-0.50*	+0.36	+0.30	+0.21
All manured treatments	-0.39	+0.57†	+0.47	+0.39
All unmanured treatments ..	-0.43*	+0.55†	+0.40	+0.78†
Unmanured, large planting material	-0.07	+0.13	+0.44	+0.74†
Manured, large planting material..	-0.01	+0.72†	+0.62*	+0.68*
Unmanured, small planting material	-0.74*	+0.50	-0.27	+0.75†
Manured, small planting material..	-0.39	+0.47	+0.66*	-0.05

* Significant at $P=0.05$. † Significant at $P=0.01$.

The significant correlations in the upper half of the Table are mainly due to the large effects of manure and of size of planting material and have not necessarily any direct bearing on the effects of spacing. Further, no importance can be attached to the significant negative correlation between bulb weight and phosphate content of the leaves on the "unmanured, small planting material" plots (as the phosphate content itself did not show a significant difference) and the significant values under K₂O and CaO do not, with our present state of knowledge, contribute materially to a causal explanation of the effects of spacing on bulb size. The correlations between nitrogen content and bulb size are seen to be significantly positive whenever nutrient supplies are poor and/or the concentration of daughter bulbs great, due to the planting of large bulbs. Thus the nitrogen data do appear to offer a partial causal explanation of the variation in bulb size caused by spacing and changes in the size of the planting material on these plots. On the "manured, small planting material" plots, however, there is no evidence that the nitrogen supply is restricted even when the plants are closely spaced. Nevertheless daughter bulb weight on these plots is very dependent on the available space and it is apparent that spacing effects not connected with competition for nitrogen are operating in this experiment. Their nature cannot be stated with certainty, although competition for water may have occurred, but least severely on the "small planting material" plots.

(B) *Globe Beet.*

(i) *Manurial effect.* Table VII shows the effect of the manurial treatment on the composition of the leaves.

TABLE VII.

Composition of Globe Beet leaves. Constituents as percentage of dry matter.

Treatment.	P ₂ O ₅	K ₂ O	CaO	N ₂
Manured	0.78*	5.67*	3.72	3.80*
Unmanured	1.05	4.76	3.62	3.57

* Difference significant at $P=0.05$.

The manurial effects found are generally similar to those in the shallots.

(ii) *Spacing effects.* Neither row distance nor thinning distance significantly affected the contents of phosphate, calcium or potash in the leaves, but both affected the nitrogen content of the leaves significantly on the unmanured but not on the manured plots.

TABLE VIII.

Nitrogen (as per cent. of dry matter) in leaves of beet grown at several spacings.

Manurial treatment.	Row distance.			
	9 in.	12 in.	18 in.	24 in.
Manure	3.45	3.72	4.02	4.02
No manure	3.18*	3.51	3.75	3.85
	Thinning distance.			
	2 in.	4 in.	6 in.	
Manure	3.88	3.57	3.95	
No manure	3.35*	3.52	3.85	

* Spacing effects significant at $P=0.05$.

As with the shallots, wide spacing causes an increase in the nitrogen content of the leaves on the unmanured plots and hence has an effect similar to that of manuring. Again the correlation coefficient calculated to express the relationship between root size and nitrogen content of the leaves is significant for the unmanured treatments ($r=+0.819$, $P=0.01$), but not on the manured plots ($r=+0.456$). Hence, whilst on the unmanured plots competition for nitrogen might be advanced as a causal explanation of the effects of close spacing on growth, this explanation would not hold for the manured plots where, however, the dependence of root weight on available space is still great. Further, whilst the effect of manuring on root weight is very slight, the effect on the nitrogen content of the leaves is considerable, whilst the effect of spacing (on the unmanured plots) on the root size is proportionately much greater than on the nitrogen content of the leaves. We come to the conclusion here (as with the shallots) therefore, that the effects of spacing on growth are only to a slight extent due to the close spacing resulting in competition for nutrients. It is unlikely that competition for water was important with the beet. The experiment was carried out in 1948, when the rainfall from mid-June onwards was unusually heavy, and although we have some evidence (Warne, 1951b, p. 302) that

mutual shading of the closely spaced plants resulted in a reduced leaf efficiency, this effect again is slight. The major effect of close spacing so far as the foliage was concerned was to reduce the weight of leaves per plant (Warne, 1951b, p. 300).

CONCLUSIONS.

The general conclusion reached is that whilst the chemical data provide evidence that, on unmanured plots, close spacing causes competition for nutrients (especially nitrogen), which results in a lowered content of nitrogen in the foliage, this cannot be the main causal factor in the effect of spacing on plant growth. On manured plots, where the spacing was without significant effect on the nitrogen content of the leaves, the general dependence of plant size on available space remained. A closer approximation of sampling and harvest dates might have provided more conclusive evidence of the importance of inter-plant competition for nutrients, but leaf senescence, preceding harvest, makes late sampling of the leaves difficult. It is possible too that some of the spacing effects and correlation coefficients which failed to reach a significant level would have done so had a greater precision in experimental procedure been attained. We cannot assume this to be so, neither can we assume (although it is possible) that estimation of the nitrogen fractions in the foliage in addition to total nitrogen would have contributed materially to an explanation of the spacing effects. So far as the data presented here and the observations reported previously (Warne, 1951a and b) are concerned, we are forced to the conclusion that the effects of spacing on growth are not solely or even mainly the result of inter-plant competition for water, nutrients or light, a conclusion similar to that of Mann and Barnes (1947, 1949) who, in considering the competition between barley and weeds, state "There seems to be no doubt of the effect of one plant on the other even though they are grown in the presence of ample supplies of water, plant food, etc."

SUMMARY.

1. Growth and chemical data for shallots and globe beet grown at two manurial levels and twelve spacings are presented and discussed.
2. Manuring (and size of planting material for shallots) affects the composition of the foliage. Spacing affects the composition of the foliage, but the only consistent effect is on the unmanured plots, where close spacing reduced the nitrogen content of the leaves.
3. On unmanured plots (and with shallots on the manured plots of large planting material) the nitrogen content of the leaves is positively correlated with root (beet) or bulb (shallot) weight. On the remaining manured plots no such correlation exists, although the dependence of size on available space remains.
4. The conclusion reached is that competition for nutrients plays a minor part only in the effects which spacing has on growth.
5. It is not possible satisfactorily to explain the observed effects of close spacing in restricting growth in terms of competition for water, light or for any of the nutrients estimated.

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SPACING EXPERIMENTS ON VEGETABLES

VI. A COMPARISON OF THE RESULTS OBTAINED IN 1948 AND 1949 IN EXPERIMENTS ON THINNING WITH ROOT CROPS IN CHESHIRE, WITH SUGGESTIONS AS TO DESIRABLE PLANT POPULATIONS FOR THESE CROPS

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SOME of the implications of spacing experiments carried out at the University of Manchester, Jodrell Bank Experimental Station, Lower Withington, Cheshire, in 1948 have already been reported (Warne, 1951a, b, c). The conclusions which were presented were necessarily tentative, based as they were on a single year's observations. A repetition of some of these experiments, slightly modified where necessary, in 1949, allows us to suggest desirable populations for root crops which subsequent work does not appear to contradict.

WEATHER OF 1948 AND 1949.

The years 1948 and 1949 provided a great contrast in summer weather and it is likely, therefore, that where agreement between the experimental results for these two years was obtained, the conclusions which can be drawn will have a fairly wide application. Rainfall and sunshine records taken at Ringway Airport for the months May to August are summarized in Table I.

TABLE I.

Weather Records at Ringway Airport.					
Year.		May.	June.	July.	August
1948	Inches of rain	1.30	4.52	3.06	4.48
1949	Inches of rain	4.22	0.94	2.13	1.98
1948	Hours of sunshine	245	161	170	89
1949	Hours of sunshine	233	241	181	192

Elsewhere (Warne, 1951a) it has been pointed out that inter-plant competition with beet and carrots had little effect on plant size until July and, as most of the experimental crops are harvested in September, it is on the critical months of July and August that interest is centred. In 1948, July and August provided an excess of 1.47 in. of rain over the 9 years' average, following a wet June with 2.09 in. of rain above the average; the late summer provided no extended period of dry weather. The driest period of the summer was 6th to 19th May with 0.02 in. of rain and the only other fortnight period with less than 0.50 in. of rain was 15th to 28th July (0.46 in.). In 1949, the July and August rainfall totals at 4.11 in. were 1.96 in.

below the average and followed a dry June with a deficit of 1.47 in. of rain. Extended dry periods included 10th June to 8th July with 0.13 in. rain (the preceeding fourteen days gave 2.43 in. of rain) and 13th to 26th August, 0.30 in. (following a three week period with 1.40 in. only). The sunshine records for 1948 show July and August to be relatively sunless with a deficit of 68 hours, following a dull June with a deficit of 46 hours. July and August 1949 provided 46 hours of sunshine above the average, following a sunny June which gave an excess of 33 hours of sunshine over the average.

So far as the summer period is concerned, 1948 may be classified as wet and sunless, and 1949 as dry and sunny.

EXPERIMENTAL PROCEDURE.

The experiments were similar in arrangement and character in the two years (Warne, 1951b and c), and generally five spacings were employed, randomized in blocks with five or six replications. They concerned globe beet, long beet, parsnips and carrots (two types) and, with the few exceptions noted later, sowing and harvesting dates did not differ by more than a few days in the two seasons and the thinning distances and other cultural operations were similar in the two years. It is manifestly not possible to ensure exact equality of soil fertility in the two seasons, but it is not thought that soil fertility differences account for more than a small part of the observed seasonal effects.

EXPERIMENTAL RESULTS.

In assessing the practical significance of the results it is necessary to consider data or statistics relating to (a) the plant populations obtained, (b) the yields, (c) the relation between root size and available space, and (d) the population required to give maximum yields in each of the two seasons.

Plant populations obtained.

Table II shows the mean values obtained with the extremes of thinning distances employed and not the extreme values for individual plots.

TABLE II.

Range of plant populations obtained in spacing experiments on vegetables, in 1948 and 1949, in thousands per acre.

Vegetable.	Row distance.	1948.	1949.
Globe Beet Variety Crimson King	9, 12, or 18 in.	65.3 to 239.6	56.0 to 148.4
Long Beet Variety Exhibition Black	18 in.	70.3 to 183.8	62.2 to 134.8
Carrots Variety Early Wonder, 1948 Variety Early Nantes, 1949	18 in.	66.5 to 236.8	83.0 to 290.4
Carrots Variety Altrincham	18 in.	60.1 to 145.2	75.7 to 326.8
Parsnip Variety Tender and True	18 in.	49.7 to 127.3	47.9 to 160.4

The minimum figures for the two seasons show fair agreement, but the maximum figures for beet, Altrincham carrots and parsnips in the two years do differ. Germination of the Altrincham carrots in 1948 was known to be poor, but that of the beet in 1949 would, on the basis of visual observation, have been considered satisfactory. Nevertheless, the maximum population obtained in 1949 was much less than that of 1948, although the nominal thinning distance was the same.

Yields.

The yield data presented are the yields of "large" roots (minimum diameters Globe beet, $1\frac{7}{8}$ in.; Long beet, $1\frac{5}{8}$ in.; carrots, $1\frac{1}{8}$ in. and parsnips, 2 in.)* and represent the mean values for those plots giving the maximum yields (within the limits of experimental error).

		<i>Yields of large roots in cwt. per acre.</i>	
		1948.	1949.
Globe beet, variety Crimson King	..	370	413
Long beet, variety Exhibition Black	..	244	348
Carrots, variety Early Wonder, 1948			
or Early Nantes, 1949 ..		278	95
Carrots, variety Altrincham..		155	298
Parsnip, variety Tender and True	..	313	259

The higher yields of beet in 1949 confirm the popular belief that beet are particularly responsive to abundant sunshine. The lower yields of parsnip in 1949 may have been due to the autumn prolongation of the dry weather of that year (less than 1.0 in. of rain fell in September, and this followed three months with an accumulated deficit of 3.43 in.). The low yields of Altrincham carrots in 1948 and of Early Nantes carrots in 1949 are in part at least the result of early lifting, decided on because of much splitting, accompanied by bolting with the variety Altrincham.

Response of individual plants to changes in the available space.

This relationship has been examined by calculating the regression of mean root weight on available space expressed in inches of row per plant and this procedure has been followed for the 1949 data. The values presented here for 1948 differ in some respects from those reported elsewhere, as, in order to make the figures for the two years comparable, data referring to plants differently treated have been omitted from the calculations.

In this table the index figure is a measure of the response of the plant to a change in the space available for its growth. Thus an index of 1.00 would indicate that, over the population range tested, a doubling of the area available per plant resulted in a doubling of the root weight. Conversely an index of 0.0 would show that root weight was independent of the area allotted to the plant. When root weight is exactly proportional to the area available, then yield per unit area is independent of changes in the plant population; whereas, when root weight is independent of the available area, yield is proportional to the number of plants present.

* These grading limits were settled on the basis of the size of root acceptable in the Manchester market and before the publication of the Ministry of Agriculture Marketing Leaflet No. 102, 1948.

TABLE III.

Regression of mean root weight in ozs. (W) on available row space in inches (S) (18 in. rows, except that values for Globe beet in 9 in., 12 in. and 18 in. rows are calculated on a 12 in. row basis).

	Mean root weight (W).	
	1948.	1949.
Globe beet	$1.99(S)^{0.70}$	$1.76(S)^{0.88}$
Long beet	$2.03(S)^{0.70}$	$2.21(S)^{0.89}$
Carrot, variety Early Wonder	$1.91(S)^{0.50}$	—
„ Early Nantes	—	$0.89(S)^{0.31}$
„ Altrincham	$2.30(S)^{0.37}$	$2.15(S)^{0.53}$
Parsnip	$2.95(S)^{0.64}$	$1.72(S)^{0.95}$

In fact, the position found lies between these two extremes and is somewhat complicated by the fact that, in practice, it is not total yields of roots that are of interest, but the yields of roots of an acceptable (saleable) size.

In 1949, with one exception (short carrots), there was a greater dependence of root size on available space than in 1948. These changes accompany an increased yield of beet and a decreased yield of parsnips. The increased yield of beet was the result of an increased growth of the plants that was most marked at the widest spacings; but the decreased yield of parsnips resulted from a decrease in the growth of the plants, the decrease being relatively greatest at the closest spacings. This may have been the consequence of a differing complex of factors operating as a limit to growth in two years. Thus we have some evidence (Warne, 1951b and c) that mutual shading may have limited the growth of the closely spaced beet in 1948. There was no suggestion of any such effect in 1949.

Populations giving the maximum yields of "large roots".

Generally it is possible to find a range of populations over which, whilst the "total" yield of roots increases, the yield of large roots remains unchanged. This position arises because, as the plants are more closely spaced, plant size decreases, so that a higher proportion of the increased total yield is rejected as being unsaleable. The range of populations which give these maximum yields is considerable, and has shown a high degree of constancy in the two years of these experiments.

Globe beet. Maximum yields were, in 1948, obtained with 120,000 to 240,000 plants per acre (highest density tested), whilst, in 1949, the corresponding range was 74,000 to 148,000 (highest density tested). The 1949 results, obtained with yields higher than in 1948, fall more closely into line with those of 1948 if we eliminate from the yield data roots of a diameter over $3\frac{1}{2}$ in.* Maximum yields of roots of diameters $1\frac{7}{8}$ in. to $3\frac{1}{2}$ in. were obtained in 1949 within the population range 110,000

* Maximum diameter suggested by the Ministry of Agriculture (Marketing Leaflet, No. 102, 1948).

to 148,000 per acre. As the higher yields of 1949 were due to an increase in the mean root weight, it is probable that a further increase in the population to 240,000 (the 1948 maximum) would not have had undesirable effects on the yield.

Long beet. In neither year, with the variety Exhibition Black, did the variation in plant population tested significantly affect the yield, so that full yields of large roots appear to be ensured with plant populations between 70,000 and 135,000 per acre. No reduction in yield followed either a reduction in the population to 62,000 or an increase to 184,000 in the one year when these populations were obtained.

Parsnips. The range of populations giving maximum yields in each of the two years under review was 59,000 to 86,000 per acre. A higher population (160,000) caused a reduction in the yield of large roots in 1949. In that year, no population between 86,000 and 160,000 was tested and it is probable that the true maximum permissible figure lies between these limits. In 1949, but not in 1948, as few as 48,000 plants per acre sufficed to give the maximum yield.

Short carrots. In both years the highest yields were obtained with the highest population tested, and it is likely that not less than 290,000 plants per acre are desirable.

Long carrots. In 1948, the highest yield was given with the highest population tested (145,000 per acre) and, in 1949, within the population range of 195,000 to 325,000 plants per acre; it is probable therefore that not less than 195,000 plants per acre are desirable, and that at least 325,000 plants per acre are permissible.

On the basis of these results it is possible to suggest for the crops tested either (a) an "optimum" population range or (b) a minimum value below which the population should not fall if maximum yields are desired. The "optimum" is the range of populations which gave maximum yields in each of the two years. It is probable that the true optimum had a greater range than given. Thus, the optimum

TABLE IV.

Suggested desirable populations in thousands per acre for root crops in Cheshire.

	Probable minimum permissible.	"Optimum" populations.	Population which is probably permissible.
Globe beet	—	120-150	240
Long beet	—	70-135	180
Short carrots	290	—	—
Long carrots	195	—	325
Parsnips	—	59-86	100?
<i>No. of plants required per foot of row in 18 in. rows.</i>			
Globe beet	—	4.13-5.16	8.25
Long beet	—	2.41-4.64	6.20
Short carrots	10.0	—	—
Long carrots	6.72	—	11.2
Parsnips	—	2.03-2.96	3.44
<i>No. of plants required per foot of row in 12 in. rows.</i>			
Globe beet	—	2.75-3.44	5.50
Long beet	—	1.60-3.09	4.13
Short carrots	6.66	—	—
Long carrots	4.48	—	7.47
Parsnips	—	1.35-1.97	2.29

range for parsnips evaluated in this way is 59,000 to 86,000 plants per acre, but the true upper limit probably lies between 86,000 and 160,000. In other cases the limit given for the optimum represents the maximum or minimum population obtained in each of the two seasons and may not represent the true limit.

These values are given in Table IV, which also shows the numbers of plants per foot of row (for both 18 in. and 12 in. rows) required to give these populations.

DISCUSSION.

The discussion of the experimental results may at this stage centre on the data presented under the heading of "populations giving the maximum yields of large (saleable) roots"; the results have a two-fold interest in relation, firstly, to experimental procedure and, secondly, to horticultural practice.

The establishment of the range of plant populations that can be depended upon to give maximum yields enables many horticultural experiments to be carried out with an added degree of precision. Variety trials and manurial experiments, provided they are conducted within the permissible population range, need not have their interpretation complicated by differences in germination or by the effects of manurial treatment on seedling survival.

We have suggested various plant populations as being desirable for root vegetables if maximum yields are to be obtained with certainty. They are based on the results of experiments carried out in two years, in which the weather differed markedly, but in a single locality. Nevertheless, they may well prove applicable to other soils of high fertility used for vegetable growing in the North-west of England. The optimum population figures are not put forward with any suggestions of finality. Further work will probably show the necessity for modifying them, but they may form a basis for discussion. Additionally, it should be pointed out that populations in excess of or less than the optima suggested do not necessarily result in decreased yields—but they may do so. Although the results obtained are of practical interest, their interpretation in relation to the present day practice of commercial horticulture is beset with difficulties imposed on us by lack of precise knowledge of vegetable culture.

Practically, we may consider the suggestions put forward in relation to spacings recommended in horticultural writings, and to the populations attained in horticultural practice. Horticultural literature abounds with suggestions as to desirable sowing rates, row distances and thinning distances, but is peculiarly devoid of any data about the plant populations obtained. Generally row and thinning distances suggested are such as to give populations less than these experiments indicate to be desirable. Thus for topped beet, row distances suggested vary from 18 in. to 24 in. (Hoare, 1945; Johnstone, 1948; Oldham, 1950) and thinning distances from 2 in. to 6 in., giving a theoretical range of populations from 44,000 to 174,000 per acre. We find, however, that with a 2 in. thinning distance for beet, we obtain only from 40 to 70 per cent. of the theoretical number of plants, and with the former value a nominal 2 in. thinning distance in rows 18 in. apart fails to give the population of plants which the experiments described suggest as the minimum desirable. For parsnips, an 8 in. thinning distance is suggested for rows 12, 15, 18 or 24 in. apart (Hoare, 1945; Johnstone, 1948; Oldham, 1950). Assuming the theoretical stand of plants to be obtained, then only with 12 in. rows would the population

attain what these experiments indicate as the minimum desirable. With carrots, however, sowing at the rate of 4 lb. of seed per acre would, assuming 300,000 seeds to the pound (Mercer, 1948), almost certainly give a population exceeding the suggested minimum.

The results presented, therefore, do not lend support to suggestions about desirable spacings for beet and parsnips made in horticultural literature, but show better agreement for carrots.

It is not possible to say how closely the provisional conclusions presented agree with those of progressive commercial growers. It is not improbable that they have by a different method reached conclusions similar to those now advanced, although they would not express them so precisely. We cannot assume this to be so, however. Research on fruit culture has shown how incorrect were the opinions held by growers fifty years ago on the spacing of bush apples, and a similar state of opinion may well exist with vegetables now. Only an enquiry in the field can determine this, and help to determine also how far deviations from optimum plant populations are the result of lack of knowledge, or of deliberately sacrificing yield to convenience of cultivation, e.g. by using widely spaced rows, or of uncontrolled "accidents" (poor germination, pest damage, etc.).

SUMMARY.

1. The results of thinning experiments on beet, parsnips and carrots in two years are compared.
2. On the basis of the results obtained, certain ranges of plant populations are suggested which appear desirable for these crops if maximum yields are to be assured on fertile soils in the North-west of England.

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BIOLOGY OF SOME PREDATORY INSECTS AND MITES ASSOCIATED WITH THE FRUIT TREE RED SPIDER MITE (*METATETRANYCHUS ULMI* (KOCH)) IN SOUTH-EASTERN ENGLAND*

I. THE BIOLOGY OF *BLEPHARIDOPTERUS ANGULATUS* (FALL.) (HEMIPTERA-HETEROPTERA, MIRIDAE)

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INTRODUCTION.

THIS study was commenced in 1945, in relation to the investigation, initiated in 1943, into the control and bionomics of the Fruit Tree Red Spider Mite in Essex. Observations and experiments have been made in many Essex and Kent orchards.

Austin and Massee (1947) found in 1944 that, in July, mite populations were markedly reduced in an orchard where oil washes were being tested; this reduction obscured any possible differences between the trees under various treatments and the control trees, and this orchard could not be used for future trials because there were insufficient mites. Large numbers of the Mirid bug *Blepharidopterus angulatus* (Fall.) were present at the time, and it was later confirmed that they were largely responsible for this decline in numbers of the mite. Between 1944 and 1950 almost fifty species of insects and mites have been found that are to some degree predacious on the red spider mites. Some of these seldom appear, and less than ten species occur regularly and plentifully in commercial orchards in South-eastern England. It is well known that populations of insects fluctuate and change over the years, and that a variation in conditions can lead to an alteration in the importance of the various species. It is therefore desirable to study in detail all the species involved, even although many may be of little or no economic significance.

It is generally accepted that, in England, the original development of the Fruit Tree Red Spider Mite as a pest of economic importance was connected with the introduction of routine winter spraying with tar oil washes between 1920 and 1930. Massee and Steer (1929) recorded that tar distillate washes were killing Anthocorid bugs known to feed on the red spider mite. These oil washes depleted the numbers of many predacious insects which normally hibernated as adult insects on the trunks of the trees or in vegetation beneath. At that time tar oils were used at a strength of from 8 to 10 per cent. and still contained tar acids. Their use killed grass and weeds beneath the trees, and all moss and lichen growing on the bark, that had given cover for many species of hibernating insects and mites. Between 1930 and 1940, methods of spraying were improved and applications of both winter and summer sprays became routine measures. Throughout that time the red spider mite steadily multiplied. Pickett, Patterson, Stultz and Lord (1946) give a similar account of

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the increase of the same species of mite in Canada. Although, by looking back, it is easy to follow the development of this species into an economic pest, at the time when it was actually happening, the causes were not apparent. During the past few years, however, the widespread use of highly potent synthetic insecticides has still further increased the mites and this has been noted by many workers throughout the world. DDT, the most widely used of these insecticides, not only kills most of the active predators without affecting the mites, but leaves a residual toxicity. Thus for several weeks after the initial application has killed off all the predators, none hatching within the orchard or flying in from the outside are able to survive. In this country, repeated warnings of the harmful nature of DDT towards beneficial insects have led to restrictions in its use in orchards to the pre-blossom period, but in other parts of the world it is used throughout the summer season. It is the high toxicity of this insecticide, and equally its residual effect, that make it dangerous where phytophagous Tetranychid mites are present. Even more recently the organo-phosphorus insecticide, parathion, has been used widely against a variety of pests. It is true that the actual application, unlike that of DDT, results in some control of mites, but a very rapid build-up of mites follows after three or four weeks, due to an almost complete elimination of the natural enemies. This capacity of the mite to build up if there is no controlling factor has been mentioned by Austin and Massee (1947), and the details of the life history described by Blair and Groves (1952) show that this is due to the number of generations that follow quickly on each other. Predators comprise the most important means of natural control, and are removed by applications of modern insecticides, especially when repeated over a number of years.

The main part of this study has been made in commercial orchards, as a part of the investigation into the economic control of the red spider mite. Cultural practices seriously interfere with natural conditions and, therefore, observations have been made in a neglected orchard, where there was no spraying, pruning or cultivation, and so a minimum of interference. These field observations were accompanied by laboratory studies of the details of the life histories of the species involved, of the number of mites consumed by the various stages of each species, and of rearing unidentified species.

Blepharidopterus angulatus (Fall.) originally focused attention on the importance of natural enemies in this part of England, and subsequently it proved to be the most consistent and numerous predator throughout orchards here. It had not previously been studied in this country, and only to a limited extent in other European countries, where it was not considered to be a beneficial species. For these reasons particular importance was attached to the study of the biology of *Blepharidopterus angulatus* (Fall.) and a detailed account of this insect follows. Part II will describe the other predacious insects and mites which occur in orchards and this will be followed by a general survey of the position of predators in orchards in relation to the spraying programme.

HISTORY.

Blepharidopterus angulatus was originally described by Fallén in 1807 as *Lygaeus angulatus*, and subsequently was often called *Actorhinus angulatus*. It has been recorded throughout Europe, and from Siberia, Turkestan and Algeria (Oshanin, 1909). There is one record only from North America, of two females identified in

Nova Scotia by Knight (1922). In Great Britain it has been captured in 42 counties of England and Wales, and also in Scotland and in Ireland (Bedwell, 1945).

Several European workers have recorded this species on apple and in England it was found in the Wisbech district by Petherbridge and Husain (1918) and by Fryer (1929). It was first noted as a predacious species in Essex in 1944 (Austin and Massee, 1947).

MORPHOLOGY.

Egg.

The egg is whitish-cream and opaque, with a smooth surface. It is a typical Mirid egg (Fig. 1), and narrows only slightly to form the neck. The egg cap is

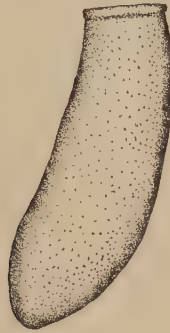


FIG. 1.

Egg of *Blepharidopterus angulatus* (Fall.) $\times 45$.

darker than the body of the egg, except for the white oval rim; the cap is the only part of the egg visible in the tissue of the young apple wood (Fig. 2, Plate I). Thirty eggs dissected from apple shoots were measured, the average size being: length 1.02 mm.; greatest width 0.35 mm.; greatest width of egg cap 0.23 mm.

Nymphs.

There are five nymphal instars which are easily distinguishable from each other by size, and in the later instars by the degree of development of the wing buds (Fig. 3). In the second instar the mesothorax is wider and longer than the metathorax; in the third instar small wing pads appear on the mesothorax, which in the fourth instar extend to the second abdominal segment. In the fifth instar the wing buds extend to the fifth abdominal segment; they are dark green until one or two days before the final moult, when the posterior region of each bud becomes almost black. *B. angulatus* may be diagnosed by the presence of a black region at the proximal end of each tibia, which has led to the adoption of the popular name, "Black-kneed Capsid"; this is characteristic of all instars of the insect, and prevents confusion with other Mirid species on fruit trees. The only other species similar in this character is *Plagiognathus arbustorum* (F.), which has very similar black "knees" when it hatches; after a few days, however, the characteristic markings of this species appear in the form of a row of black spots and spines on the tibiae, and black lines along the margins of the femora; after the first instar these markings are quite distinct and distinguish clearly between the two species.

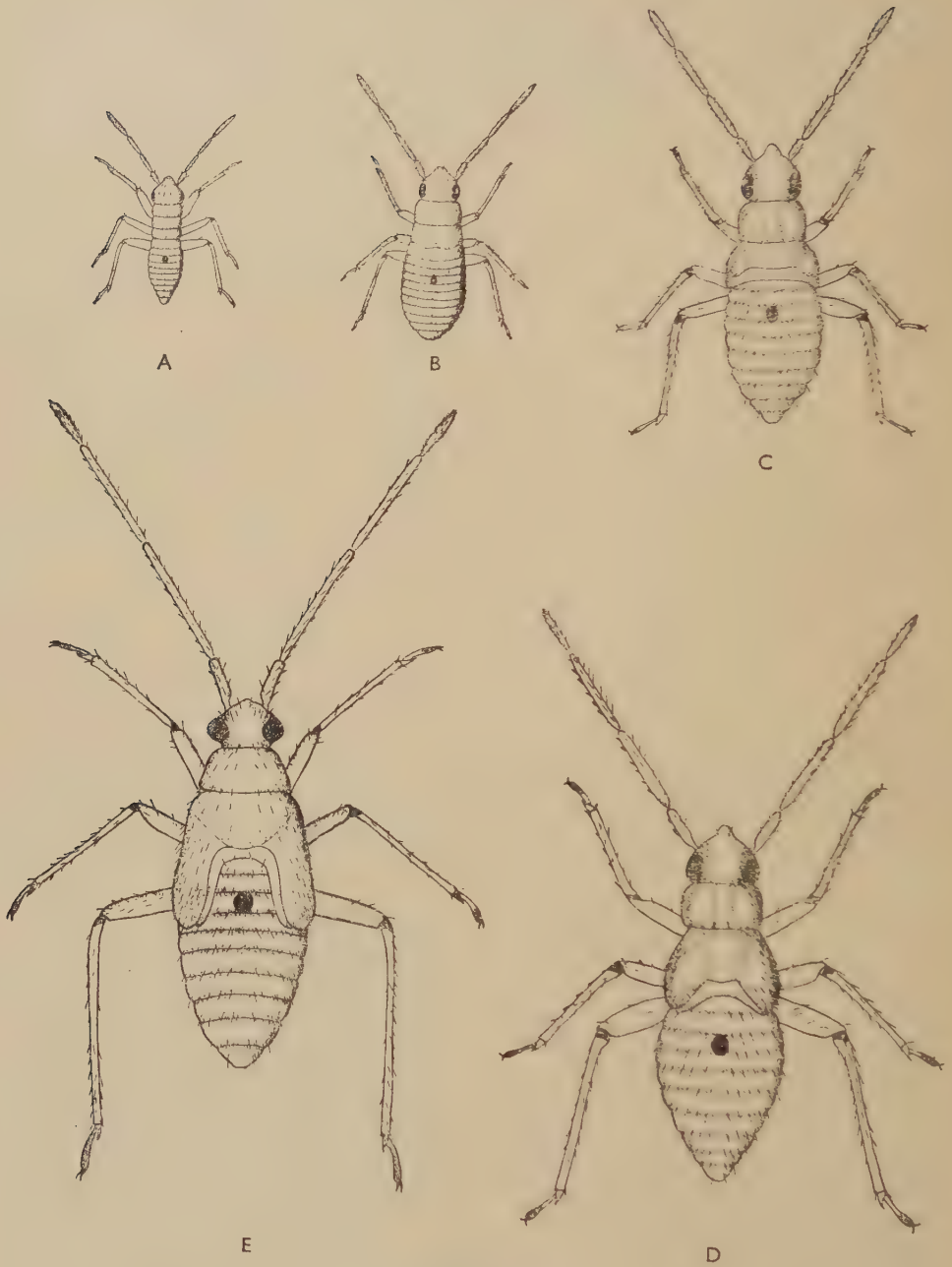


FIG. 3.
Blepharidopterus angulatus (Fall.). A-E, nymphs of I-V Instar. $\times 15$ approx.

The Black-kneed Capsid nymphs are yellow to green in colour, with red eyes ; the tarsi are dark, with black claws, and the legs are pale. The antennae are long, the terminal joint being slightly darker than the rest. The orange abdominal gland shows clearly through the dorsal body wall of the third abdominal segment in all instars, opening dorsally between segments 3 and 4.

TABLE I.

Blepharidopterus angulatus (Fall.). Measurements (mm.) of 25 individuals of each nymphal instar.

		Instar I.	Instar II.	Instar III.	Instar IV.	Instar V.	
						♂	♀
Average length of antenna	Joint 1	0.12	0.19	0.28	0.44	0.50	0.46
	Joint 2	0.18	0.30	0.50	0.88	1.19	1.14
	Joint 3	0.20	0.33	0.55	0.88	1.12	1.11
	Joint 4	0.31	0.37	0.44	0.54	0.57	0.56
	Total	0.81	1.19	1.75	2.72	3.38	3.27
Average length of body		1.3	1.7	2.3	3.0	3.8	

Imago.

The imago has been described by Douglas and Scott (1865) but the differences between the two sexes have not previously been noted. On the average, the males are longer from the head to the extremity of the elytra, and have considerably longer antennae than the females (Fig. 4). The basal antennal joint is dark brown

TABLE II.

Blepharidopterus angulatus (Fall.). Measurements (mm.) of the antennae of the imagines.

			Average length of antenna of 30 individuals.				
			Joint 1.	Joint 2.	Joint 3.	Joint 4.	Total.
Male	..	..	0.77	1.97	1.91	0.62	5.27
Female	..	..	0.64	1.66	1.50	0.60	4.40

ventrally along its length in the male, but paler in the female with only a faint line along the ventral surface ; the second and third joints of the male antenna are darker than those of the female. The eyes of the male are dark red and almost meet ventrally, those of the female are paler and more widely separated. The whole of the body, including the wings, is darker in the male, the general colour being a rich green whereas the female is yellowish-green.

LIFE HISTORY.

Very little has been published concerning the life history of *B. angulatus* ; the overwintering egg stage is mentioned by Abraham (1937), Speyer (1933) and

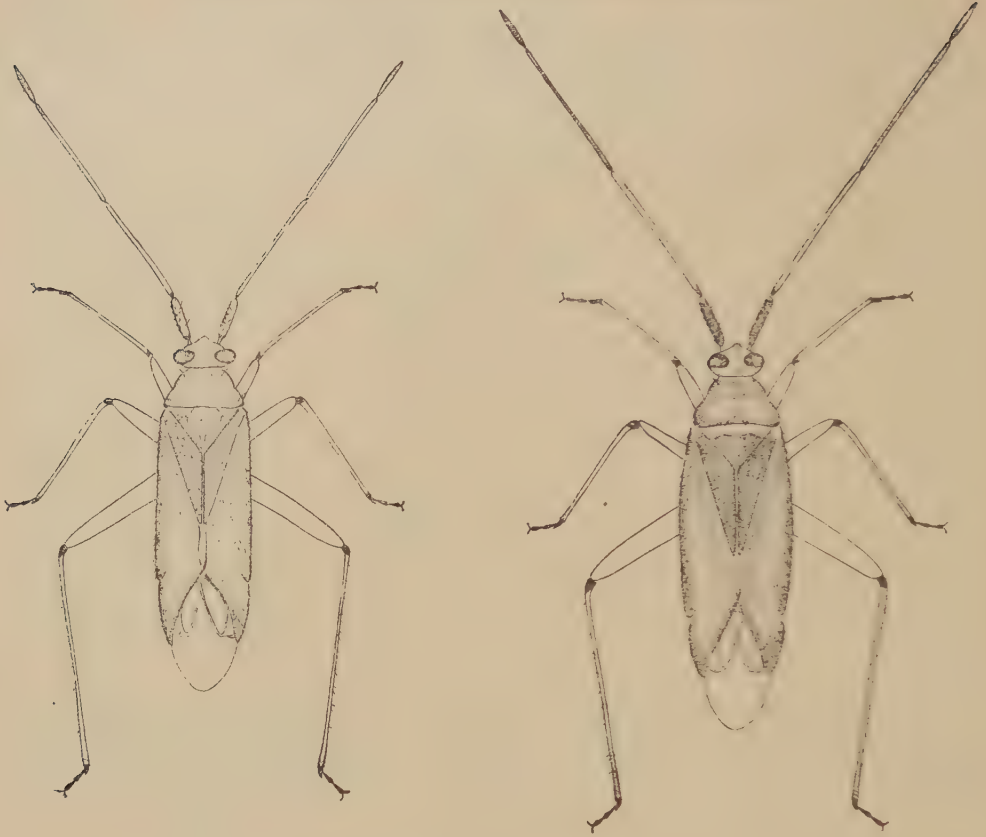


FIG. 4.
Blepharidopterus angulatus (Fall.).
× 10 approx.

Adult female.

Adult male.

Kullenberg (1944), and brief notes on the nymphs are given by Butler (1923), Speyer (1933) and Kullenberg (1944).

Rearing.

This species, in common with many Mirids, is very difficult to breed in the laboratory because it is delicate and is readily injured. The highest mortality occurs when moulting, especially in hot weather and, when the temperature exceeds 90° F., mortality may be very high. Each individual must be kept separately or they may devour one another when in confined conditions. The nymphs were most successfully reared on a small twig of apple foliage embedded in a pot of sand, covered by a hurricane lamp glass with a muslin top. Imagines also lived successfully under these conditions, but to overwinter the eggs it was necessary to induce oviposition on living plants. Apple seedlings were used for this purpose, confined in muslin insect cages which were approximately 18" × 12" × 12". The nymphs in the lamp glasses were kept supplied with small apple twigs bearing mites, the twigs being changed frequently. The red spider mite supply was maintained on the seedlings by regular introduction of mite-infested leaves; as soon as these wilted all the

active mite stages moved from the dead leaves on to the living seedling. By this method it was possible to obtain all the eggs of the one female on one apple seedling.

Eggs.

Oviposition occurs from July to October and the eggs remain embedded in the shoot until the following May to July. There is only a brief period between the completion of hatch of the one generation and the beginning of oviposition of the next, and in some years these may actually overlap (Fig. 5).

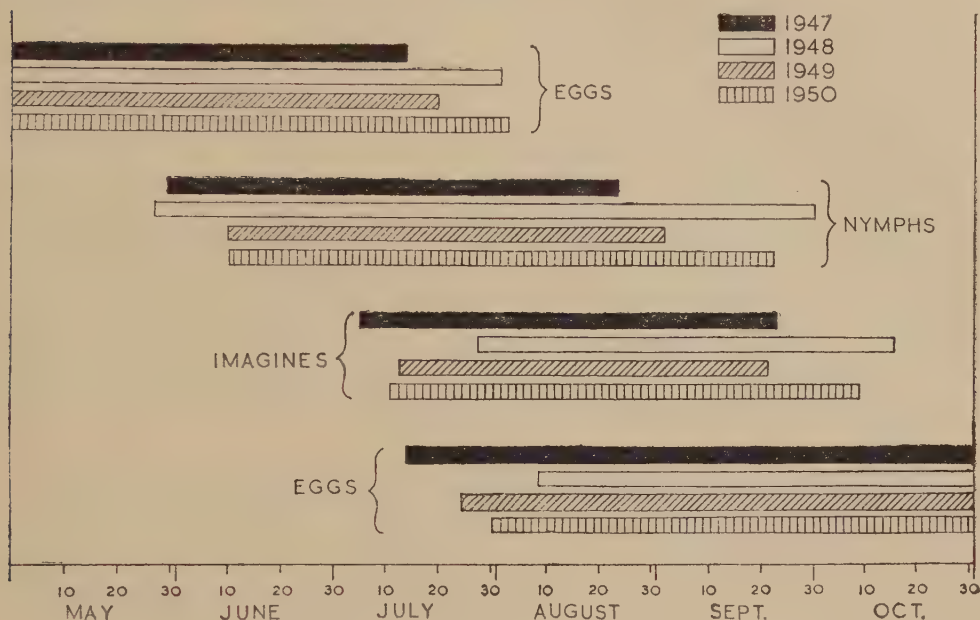


FIG. 5.
Life history of *Blepharidopterus angulatus* (Fall.).

Although oviposition occurs on a wide variety of hosts, most observations have been carried out on apple. Here the eggs are laid in the one- and two-year-old and, very occasionally, in the three-year-old wood. The proportion of eggs laid in one-year wood varies from 10 to 90 per cent. according to the season and the variety of apple. The twigs most favoured are short and succulent with unribbed surfaces. The female often selects the soft wood around the buds, and also the terminal bud region of the previous year's wood, where oviposition occurs in the bud scale scars. The egg is normally inserted for its whole length into the tissue of the shoot, only the egg cap remaining above the surface. The egg cap is easily visible, except in very young wood when it may be obscured by plant hairs. Occasionally lenticels or small wounds are selected, but more frequently a special slit is made for the purpose. Eggs are usually laid singly, but sometimes from two to four may be laid separately in a group, each egg having a distinct cavity.

An injury to the wood tissue is caused when the egg is laid, and after two or three days a typical "bump" often develops (Fig. 2) in the smooth one- or two-year-old wood, but not if lenticels, wounds or leaf scars are used. The occurrence and size

of the "bumps" vary considerably, but they are of great value in locating and estimating egg populations in the field. The cap protrudes from the side of the "bump" according to the angle of insertion of the egg. Although not a diagnostic feature this "bump" formation is typical of *B. angulatus*, and has not been observed with other Mirid species. The presence of the egg usually affects the plant tissue around its neck; a brown, hardened collar is formed and the whole egg is sometimes surrounded by hardened tissues forming an almost complete case. Occasionally eggs partially protrude from the wood, but these rarely hatch.

Hatching.

Hatching continues from the end of May until some time in July or even August, varying in different orchards and from year to year. The earliest hatching dates noted in apple orchards between 1947 and 1950 were 19th May, 21st May, 1st and 7th June, respectively, in relatively warm and sheltered places.

The peak emergence of nymphs is in June, continuing until 24th July in 1947, 29th July in 1948, 20th July in 1949, and early August in 1950. The longest period of hatching, during the four years, extended over ten weeks in 1948, when summer conditions were cooler than in 1947 and 1949 (Fig. 5). In 1948 nymphs that hatched late and were also slow in developing did not mature until October and consequently oviposition was low. Table III shows that, in the same locality, hatching started three to four weeks earlier in a sprayed orchard than in an unsprayed one, but in each year it ended almost simultaneously. Thus the hatching period begins

TABLE III.

Hatching of Blepharidopterus angulatus (Fall.) in two types of orchard.

Year.	Earliest recorded hatch.		Latest recorded hatch.	
	Sprayed orchard.	Unsprayed orchard.	Sprayed orchard.	Unsprayed orchard.
1947	19th May	1st July	18th July	24th July
1948	21st May	28th June	29th July	9th August
1949	1st June	29th June	22nd July	20th July
1950	6th June	2nd July	3rd August	2nd August

earlier and is more extended in commercial orchards, whereas hatching of the red spider mites starts more than a week later in the commercial than in the derelict orchards. There is no apparent explanation for this change in habit of *B. angulatus*. Fryer (1929) noted a change in time of hatching of another Mirid species, *Plesiocoris rugicollis* Fall., when it changed its habitat from one host plant to another. Originally an inhabitant of willow and bog myrtle, it first infested apple plantations in about 1900; whereas, on the willow, hatching took place from May to June, in apple orchards it was from April to May, four weeks earlier.

The first indication of hatching is the lifting of the egg cap from one side. The head appears first, with the two large red eyes very prominent. As the insect emerges, it leaves behind it the embryonic cuticle which often remains conspicuous in the mouth of the egg. The first instar nymph runs about actively in search of food within five minutes of hatching.

Nymphal instars.

The duration of each instar depends on prevailing weather conditions. From individuals reared in the laboratory the following data were obtained :

TABLE IV.
Blepharidopterus angulatus (Fall.). Duration of nymphal instars.

Instar	1947.		1948.	
	No. of days.	Average.	No. of days.	Average.
I.	7-9	8	6-18	11
II.	3-9	6	2-10	6
III.	3-8	5	2-6	5
IV.	4-8	6	5-9	7
V.	6-15	10	6-14	10
Total	25-44	35	27-53	39

Table IV shows that the cooler and less settled weather in 1948 resulted in a greater variation in the duration of the instars ; in general, development took longer than in 1947. Nymphs that hatched in May or early June required longer to complete their development than those that hatched later in the summer ; for example, in 1947, the average time for development of the nymphs that hatched in July was 30 days, as compared with 38 days for those that hatched in May and early June.

B. angulatus nymphs, when feeding, move swiftly backwards and forwards over the leaves, touching the surfaces with the sensitive tip of the proboscis ; this search is unsystematic and the same ground may be covered many times. When at rest, and in wet and windy conditions, the nymphs shelter on the underside of the leaf, near the base of the midrib. In windy weather they cling tenaciously and are not easily dislodged. On very hot summer days many more nymphs were found on the shady side of the tree than on the sunny side.

Imagines.

In the four years 1947 to 1950, imagines were first found in the orchard on 1st July, 27th July, 14th July and 8th July respectively. At first there is always a preponderance of males, but soon the ratio of the sexes becomes equal ; late in the summer the females predominate. The females live from six to eight weeks, although in many of the later maturing insects this length of life is not achieved. The males live from three to four weeks, and very few survive into September. Females remain active on the trees so long as leaves and mites remain, and in some years are present in October.

The fifth instar nymphs and young imagines tend to be gregarious, but this habit is in no way correlated with food supply. Copulation takes place 5 to 6 days after the final moult of the female and many mating pairs may be found on calm, warm days. The female starts oviposition 6 to 7 days afterwards. In the laboratory, up to 50 eggs were laid by each female under favourable conditions. An average number laid was found to be 43 eggs in 51 days or rather less than one egg per day. The eggs are laid spasmodically ; during the first two or three weeks they are usually laid in batches of up to twelve at a time ; each short and intensive period of

oviposition is followed by several days of active feeding before another batch is laid. Towards the end of the female's life, eggs are laid singly at the rate of one about every two days. The full egg complement was rarely laid, as dead females both from the field and laboratory still contained ova in the abdomen. Preparatory to oviposition, the female moves restlessly up and down the twig, apparently testing the surface with the tip of her proboscis. Finally she comes to rest, generally facing the base of the shoot. The saw-like blades of the ovipositor are inserted deeply into the tissue and after a short while the egg passes down between them. Afterwards the ovipositor is gradually withdrawn by moving the body gently from side to side. The whole process takes from four to eight minutes.

Feeding habits.

This species has been reported as being phytophagous by Petherbridge and Husain (1918), Fryer (1929), Speyer (1933), and Kullenberg (1944); other authorities refer only to the host plants.

In the commercial orchards it feeds mainly on the Fruit Tree Red Spider Mite, but is by no means specific in its choice and has been noted feeding on many other small insects and mites. When they are plentiful in the orchard, *Bryobia practiosa* Koch and other phytophagous mites, aphids, thrips, and occasionally predacious mites of the family Laelaptidae are readily attacked. In the absence of more suitable food, *B. angulatus* often attacks other predacious species, and has been observed feeding on larvae of *Conwentzia pineticola* End., *Stethorus punctillum* Wei., *Oligota flavicornis* Boisd. and of Syrphidae; under laboratory conditions it also attacks the more active predators like the Anthocoridae and other Miridae, but may itself fall victim to them. Cannibalism is frequent when two or more of this and other Mirids are kept together in laboratory conditions, but not when the supply of red spider mites is sufficient. When pairs of imagines are kept in the laboratory for breeding purposes the male frequently falls victim to the female, occasionally even before mating. It is possible, however, to keep a male and female together in a lampglass for four weeks if the food supply is constantly renewed.

All stages are equally predatory, but the smaller nymphs refrain from attacking the larger and more active prey. They are highly voracious and attack aphids far larger than themselves, but prefer the active red spider mite, particularly the adult females. Summer eggs of the mite are only occasionally sucked dry, and the winter eggs very rarely. When in search of food the nymphs move rapidly over the surface of the leaf, feeling with the tip of the proboscis, which is apparently the only sensitive region, no response being shown when the tarsi contact suitable food. As soon as the proboscis touches its prey the tip is applied to it and the stylets are pushed rapidly in; to allow this extension of the stylets the proboscis bends at the junction of the first two joints, the stylets separating from their groove for part of their length. If the victim struggles excessively it is held down by the predator's fore-legs. During feeding, especially of the younger nymphs, the red body fluid of the red spider mites can be seen passing up the proboscis and into the pharynx, causing the large red-brown patch frequently seen in the abdomen. Nymphs that have been feeding on aphids are green. The body fluids of the victim are completely absorbed and the empty skin is left on the leaf; if disturbed, the bug may leave the prey only partially sucked. An adult *B. angulatus* takes approximately three minutes to suck a female mite.

The effect of *B. angulatus* upon mite populations in the field is important and extensive laboratory work was carried out in the summers of 1947 and 1948 to ascertain the number of mites consumed by individuals of this species. An effort was made to record the mites consumed from the time of hatching to the death of individual bugs. Some of the nymphs died but, in each year, from a series started in June, several were kept alive through a normal life time. Large numbers of adult female mites were transferred to the leaves of small mite-free apple twigs by means of a small brush or needle; female mites were used throughout as they are more easily transferred than other mite stages from one leaf to another. The Mirid was placed on the twig and left for 24 hours, after which the corpses of the red spider mite were removed from the leaves and counted; the sucked skins adhere to the leaf and probably, during that short time in the absence of wind and rain, few were lost. The alternative method of counting the live red spider mites placed on the leaves, and subtracting the number of live ones remaining, was not practicable as the female mites sometimes migrate from the leaves. The technique adopted was repeated every 24 hours throughout the lifetime of the insect. At no time was the insect short of food, nor was it provided with any alternative prey; as each insect was kept separately, the results obtained show the consumption possible under favourable conditions.

The average total number of adult female mites consumed by females of *B. angulatus* was 3,248 in 1947 and 4,230 in 1948. Fig. 6 shows the actual consumption of mites throughout the summer by one individual female which lived for over 14 weeks.

In common with many Mirid species, *B. angulatus* takes both animal and plant food. Although under natural conditions in Essex it is essentially carnivorous, it is partially phytophagous. Nymphs and imagines have been noted sucking the leaves, but do no obvious damage to the plant tissues; they cannot be kept alive for more

TABLE V.

Feeding of Blepharidopterus angulatus (Fall.) on the Fruit Tree Red Spider Mite.

	Stage.	Number of individuals recorded.	Average no. of mites per day.	Average duration of this stage.	Total no. of mites consumed.
1947 ..	Instar			days	
	I.	11	11	8	88
	II.	6	13	6	78
	III.	6	18	5	90
	IV.	7	22	6	132
	V.	5	34	10	340
	Adult female	5	72	35	2,520
1948 ..	Instar			days	
	I.	6	5	11	55
	II.	8	7	6	42
	III.	7	12	5	60
	IV.	10	19	7	133
	V.	10	40	10	400
	Adult female	7	60	49	2,940
	Adult male	3	30	21	630

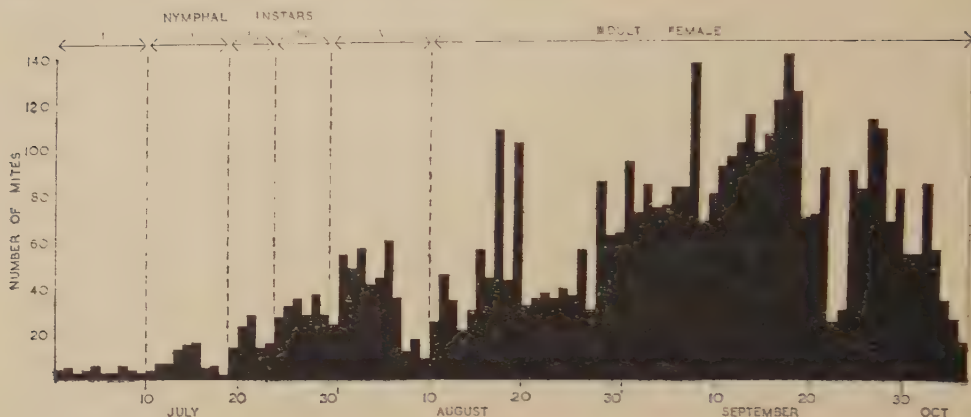


FIG. 6.

Feeding of *Blepharidopterus angulatus* (Fall.) on the Fruit Tree Red Spider Mite. Number consumed daily by one female in 1948.

than a few days on foliage alone, but introduction of a very little animal food is sufficient to support them. Fruitlets are often sucked, but the surface is not injured; later in the season *B. angulatus* is partial to rotten fruits both on the tree and on the ground.

HOST PLANTS.

The nature of the animal food supply available is far more important to this predacious insect than is the host plant. The adults fly actively in the summer and are found on many plants. Host plants are defined as those normally used for oviposition. In the fruit areas of Essex and Kent, *B. angulatus* has only been found in large numbers on apple, plum, damson, pear, cherry and walnut, and is most abundant where these are infested with red spider mites. Fewer are found on various trees and bushes of neighbouring hedges and woods. Of these the following are considered true host plants, although none are so important as the orchard trees: elm, hornbeam, oak, hawthorn, sloe, maple and hazel.

It has been reported widely and repeatedly in the European literature on *Alnus glutinosa* and *Betula alba*, and less often on *Acer*, *Corylus*, *Fraxinus*, *Lonicera*, *Prunus*, *Quercus*, *Ribes*, *Salix*, *Spiraea*, *Tilia*, and *Ulmus* (Butler, 1923; Kullenberg, 1944; Reuter, 1883). Whether it is normally predacious when living on these host plants is not known.

ACKNOWLEDGMENTS.

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PLATE I.



FIG. 2.

(a) Egg "bumps" of *Blepharidopterus angulatus* (Fall.) on twigs of apple, variety Worcester Pearmain. Slightly reduced. "Bumps" on two twigs indicated by arrows.



FIG. 2.

(b) Egg "bumps", enlarged.

SUMMARY.

An introduction is given to an account of all the predators of the Fruit Tree Red Spider Mite (*Metatetranychus ulmi* (Koch)) in Essex, of which this paper is the first part. The development of the mite as a pest is traced through the last thirty years, in relation to the introduction of tar oil spraying and the subsequent improvements in methods and materials.

The Black-kneed Capsid, *Blepharidopterus angulatus* (Fall.) is the principal predator of the red spider mite in commercial orchards. The egg, the five nymphal instars and the adult male and female of this species are described. The eggs cause the formation of a typical "bump" in the young apple wood in which they are laid in late summer; they hatch in the following May, June or July. The nymphs and imagines are predacious, although they are also partially phytophagous; counts have been made of the number of red spider mites consumed by all stages of this species under favourable conditions.

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EXPERIMENTS ON THE CONTROL OF BROWN ROT OF APPLES AND PLUMS

I. LABORATORY TESTS*

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THIS paper deals with laboratory tests of the toxicity of fungicides towards *Sclerotinia fructigena* Aderh. and Ruhl. and *Sclerotinia laxa* Aderh. and Ruhl., the fungi causing the brown rot diseases of fruit in this country. Field trials on the direct control of the diseases by fungicidal sprays will be reported later. Two progress reports have already been published (Byrde, 1949, 1950).

REVIEW OF THE LITERATURE.

General account of the brown rot diseases.

In a full account of the etiology and morphology of the brown rot fungi, which includes an exhaustive bibliography, Wormald (1935) has established that the fungi which cause brown rot of apple and plum fruits in this country are *S. fructigena* and, to a lesser extent, *S. laxa*, the latter species rarely attacking apples. In the same bulletin (pp. 41-4), Wormald dealt with some general considerations of the control of brown rot diseases. Removal of sources of infection, such as overwintering mummified fruits and cankered spurs, was stressed as being of great importance and mention was also made of the indirect control of the disease by checking insect pests and fungi which cause injuries through which brown rot may enter.

As a preliminary to the investigation of more direct attacks on these diseases by the field applications of fungicides toxic to the pathogens, an extensive programme of laboratory bioassays of fungicides was undertaken.

Methods of laboratory testing of fungicides.

In recent years the testing of fungicides in the laboratory has been extensively developed, as a method of selecting from a wide range of fungicides those likely to be of most value for trial on the limited amount of field material generally available. A comprehensive review of methods of bioassay of fungicides has been published by Horsfall (1945).

The brown rot fungi lend themselves well to such laboratory testing, since they sporulate fairly freely and their mycelium grows vigorously in culture. For example, *Sclerotinia fructicola* (Wint.) Rehm., the principal North American species, is specifically recommended by the American Phytopathological Society, Committee on Standardization of Fungicidal Tests (1943a), as a suitable test organism for spore germination experiments, although requiring the addition of a spore stimulant for satisfactory germination.

* The work published in this paper was undertaken for the Degree of Doctor of Philosophy of the University of Reading. The investigations were mainly carried out at Long Ashton Research Station, by kind permission of the Director.

The recommendations for standard techniques listed in the above paper, and in a further publication (1947), are based on extensive research throughout the world, particularly by McCallan and his co-workers at the Boyce Thompson Institute in the U.S.A. The two papers deal at length with the setting up of the tests and the interpretation of the results by means of a probit transformation.

For preliminary trials, and for testing water-soluble fungicides, the test-tube dilution technique is recommended, because of its simplicity and rapidity. Drops of a mixture of a spore suspension and the fungicidal solution are pipetted out on glass slides; the germination of the spores is recorded after a given incubation period.

For more accurate work, particularly with insoluble compounds, a laboratory sprayer technique is used. Cellulosed glass slides are sprayed with a fungicide solution (using a settling tower or horizontal sprayer) and allowed to dry. Drops of spore suspension are then pipetted out on the fungicidal deposit, germination being recorded as before.

The testing of fungicides against mycelium in an agar medium has been less developed. Although the method requires more time, Horsfall (1945) pointed out that it is valuable for use when dealing with specific fungi that do not sporulate readily. On the other hand, he considered that the presence of a large quantity of organic matter in the culture medium often interfered with the action of the fungicides, resulting in misleading data.

Palmiter and Keitt (1937) and Carpenter (1942) tested various eradicant fungicides against *S. fructicola* and other fungi by means of agar techniques. These involved the insertion of a disc of viable mycelium into an agar medium in which a fungicide had been incorporated. Their assessment of fungicidal effect was based on life or death of the fungus, and was thus purely qualitative.

A variation of the agar technique was used by Crowdy (1948) in tests of the toxicity of organic acids towards the mycelium of *Nectria galligena* Bres. He inoculated plates of toxic agar at a central point with mycelium of the fungus, and measured the increase in mean diameter of the colonies over a period of days. By comparison with data from control plates, he was able to arrive at a quantitative estimate of the efficiency of the fungicides at a given concentration.

Statistical treatment.

The statistical treatment of the data obtained follows the procedure given by Finney (1947, pp. 188-208), the principles of which may be very briefly described as follows. In tests recording levels of spore germination at different doses of the toxicant, the figures for response (i.e. percentage inhibition) are first converted to a probit scale, which, broadly speaking, measures equal increments of toxicity by equal gradations. This compensates for the inequality of response shown by the percentage inhibition figures, in which a dose increment near the 50 per cent. inhibition point is reflected by a large increase in spore mortality, while an equal increment at a higher or a lower dosage level will affect much smaller numbers of spores. Further, as the effect of additional equal doses commonly increases in a geometrical ratio, the logarithm of the dose, and not the dose itself, is plotted against this probit response.

The points plotted in this manner very frequently lie along a straight line. It follows that when three or more points have been obtained, the approximate slope

and position of the line can be fixed and expressed by a simple algebraic equation (see Appendix, Table A). Further, the dosage effective to give a response of 50 per cent. inhibition of germination (ED. 50) or 95 per cent. inhibition (ED. 95) can readily be derived from the graph. For the sprayed-slide method these dosages can be expressed as micrograms per square cm. of fungicidal deposit; or, if the test-tube technique is employed, these standard fungicidal values can be compared in parts per million (Table I).

When comparisons of a number of fungicides are needed, it is impracticable to make all the tests simultaneously. To allow for day-by-day differences in the level of resistance of the spore populations tested, it is necessary to overlap the sets of fungicides used on the different dates, as shown in Appendix, Table B. A full description of this type of lay-out and of the statistical treatment of the results is given by Yates (1936).

MATERIALS.

Fungi.

Stock cultures of *S. laxa* and *S. fructigena* were maintained on 2 per cent. potato dextrose agar.

Some difficulty was experienced in obtaining a consistent supply of spores of the fungi, but the method recommended by Wiltshire (1920) generally gave fairly good results. Conidia of *S. laxa* were obtained from 7-days-old cultures grown at 25° C. on autoclaved potato plugs previously soaked in 7½ per cent. malic acid for 72 hours. Conidia of *S. fructigena* were obtained from similar cultures, kept at 28° C., for four days, and then exposed to light under laboratory conditions for a further three days to encourage sporulation.

**Fungicides.*

The fungicides tested, classified for convenience in broad chemical groups, were as follows:

I. INORGANIC COPPER COMPOUNDS.

Copper sulphate, as an aqueous solution of the pentahydrate.

Standard laboratory Bordeaux mixture, prepared as recommended by the American Phytopathological Society, Committee on Standardization of Fungicidal Tests. (1943b).

2. ARSENICALS.

Sodium arsenite, as an aqueous solution.

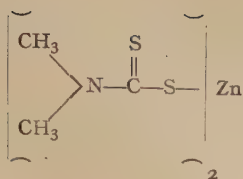
Monocalcium arsenite, as an aqueous suspension, prepared in the laboratory from arsenious oxide and calcium hydroxide by shaking them together in distilled water for twenty minutes. The ratio of lime to arsenious oxide was that required by the formula $\text{CaH}_4(\text{AsO}_3)_2$, and the compound will therefore be referred to as monocalcium arsenite, although the possibility remains that the material may be a mixture.

3. SULPHUR COMPOUNDS.

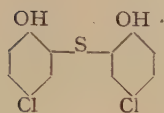
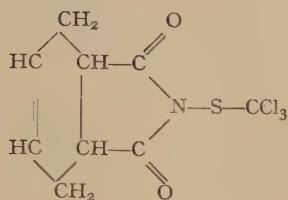
Lime-sulphur, as an aqueous solution.

Colloidal sulphur, as an aqueous suspension of a 50 per cent. wettable paste.

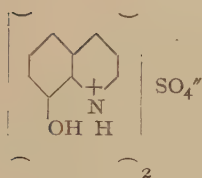
* The structural formulae of compounds marked with an asterisk are shown in Figure 1.



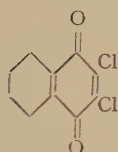
Zinc dimethyldithiocarbamate.

*Bis* (2-hydroxy, 5-chlorophenyl) sulphide.

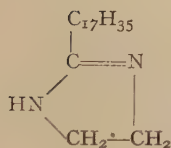
N-trichloromethylthiotetrahydrophthalimide.



8-Hydroxyquinoline sulphate.



2:3-Dichloro-1:4-naphthaquinone.



2-Heptadecylglyoxalidine.

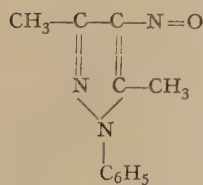
1-phenyl-3:5-dimethyl-4-nitroso
pyrazole (J.55).

FIG. 1.

Structural formulae of seven organic fungicides.

Ferric dimethyldithiocarbamate, as an aqueous suspension of the pure material, mixed with four times its weight of bentonite to disperse it.

* *Zinc dimethyldithiocarbamate*, as an aqueous suspension of a dispersible powder containing 80 per cent. of the pure material.

Zinc ethylene bisdithiocarbamate, as an aqueous suspension of a 65 per cent. preparation.

* *Bis(2-hydroxy, 5-chlorophenyl) sulphide*. A stock suspension was prepared as follows :—

<i>Bis(2-hydroxy, 5-chlorophenyl) sulphide</i>	..	0.1 gm.
Alcohol		5 ml.
2 per cent. methyl cellulose		1 ml.
Distilled water to..		50 ml.

* *N-trichloromethylthiotetrahydrophthalimide*. This compound forms the basis of a new fungicide from the U.S.A., and a stock suspension of the pure material was prepared as follows :

<i>N-trichloromethylthiotetrahydrophthalimide</i>	..	0.1 gm.
Acetone		10 ml.
2 per cent. methyl cellulose		2 ml.
Distilled water to..		200 ml.

4. MERCURIALS.

Phenyl mercury chloride. This was compounded as a stock suspension by grinding together :

Phenyl mercury chloride		10 gm.
10 per cent. sulphite lye		100 ml.

Phenyl mercury acetate, as a stock suspension or solution of a 90 per cent. preparation. Hot water was used to dissolve the material more quickly.

Phenyl mercury formamide, as a water-miscible liquid containing 3.3 per cent. of active material.

Phenyl mercury monoethanol ammonium acetate, as a water-miscible liquid containing 11.5 per cent. active material.

Diphenyl mercuric salt of di-2 : 2'-naphthyl methane—3 : 3'-disulphonic acid, as an aqueous solution of a 10 per cent. water-soluble powder containing 90 per cent. of inert material.

5. SUBSTITUTED PHENOLS AND CRESOLS.

Dinitro-ortho-cresol, as a stock emulsion containing 2 per cent. D.N.O.C. and 60 per cent. JD-2 petroleum oil, with sulphite lye emulsifier.

Sodium dinitro-ortho-cresolate, as an aqueous solution of the crude salt, which contained 60 per cent. of pure material.

Sodium pentachlorophenate, as an aqueous solution of the neutral powder.

6. SUBSTITUTED QUINONES AND QUINOLINES.

* *8-Hydroxyquinoline sulphate*, as an aqueous solution of the neutral monohydrate.

Copper 8-quinolinolate. A stock suspension was prepared by grinding together :

Copper 8-quinolinolate		10 gm.
10 per cent. sulphite lye		50 ml.

*2 : 3-Dichloro-1 : 4-naphthaquinone, as an aqueous suspension of a 50 per cent. preparation.

7. ORGANIC COMPOUNDS CONTAINING ACTIVE NITROGEN.

*Glyoxalidine acetates, as a water-miscible liquid containing 54 per cent. active material. After dilution, 0.25 gm. calcium hydroxide was added per ml. of fungicide concentrate.

Malachite green, as an aqueous solution.

*1-phenyl-3 : 5-dimethyl-4-nitroso-pyrazole ("J.55 ") was prepared by the methods described by McNew and Sundholm (1949). A 1 per cent. alcoholic stock solution was used for dilution as required. The fungicide was not reprecipitated in aqueous solutions when used at 100 p.p.m. or less.

1-(4-chlorophenyl)-3 : 5-dimethyl-4-nitroso-pyrazole ("J. 49 "), as a 1 per cent. alcoholic stock solution.

1-(4-sulphamylphenyl)-3 : 5-dimethyl-4-nitroso-pyrazole ("36.L "), as an aqueous suspension.

8. MISCELLANEOUS.

Sodium hypochlorite, as an aqueous solution of a commercial sample of hypochlorite. Chemical analysis at the time of bioassay showed that the sample contained 7.14 per cent. free chlorine.

Tar-oil, as a stock emulsion made up as follows :

Tar-oil	50 ml.
10 per cent. sulphite lye	50 ml.

Petroleum oil (JD-2), as a stock emulsion made up as follows :

Petroleum oil (JD-2)	60 ml.
10 per cent. sulphite lye	40 ml.

Copper naphthenate. This fungicide was compounded by the method recommended by Youganova (1946). This consisted of preparing an oil emulsion from the following :

Copper naphthenate	6 gm.
Grade "G" oil ("P.31") (approx. 70 ml.)	60 gm.
Bentonite	30 gm.
Distilled water to	1 litre.

The copper naphthenate was thoroughly dissolved in the oil by gentle warming and the resulting oily solution added, little by little, to a stiff paste of bentonite and water, stirring vigorously to emulsify the oil before adding a further quantity. Small amounts of water were added as necessary when the emulsion became too oily. On completion, the mixture was diluted to full volume.

Pentachloronitrobenzene, as an aqueous suspension of a dispersible powder containing 20 per cent. active material.

Dinitrocaprylphenyl crotonate has been used as a combined fungicide and acaricide in the U.S.A. Rich and Horsfall (1949) reported that, owing to volatilization of the fungicidal component from dry deposits, orthodox slide-germination tests did not show the material to advantage. In the present research it was tested in an agar medium, and made up as follows :

Dinitrocaprylphenyl crotonate (25 per cent.)	0.8 gm.
Acetone	8 ml.
Wetter	0.5 ml.
Distilled water to	200 ml.

METHODS.

Spore germination tests.

The methods used were substantially those recommended by the American Phytopathological Society, Committee on Standardization of Fungicidal Tests, (1943a).

Glassware. Glass slides were dipped in cellulose nitrate solution (2.5 per cent. in butyl acetate), and allowed to dry for at least forty-eight hours before use. Slides were incubated on glass slide-racks in 6-inch moist chambers.

Spore stimulant. Ultrafiltered orange juice, at a final concentration of 0.1 per cent., was used throughout as a spore stimulant. One sample of juice gave unsatisfactory control germination figures, which were improved by the addition of 0.2 millimolar magnesium sulphate.

The methods used in individual spore germination tests are described in a subsequent section (p. 138).

Mycelial growth tests.

The toxicity of fungicides to the mycelium of *S. laxa* was studied by determining the growth rates of cultures on 2 per cent. potato dextrose agar (pH 5.6), in which the toxicants had been incorporated. This was achieved by the addition of 0.2 ml. portions of fungicide solutions, at appropriate concentrations, to 12.5 ml. portions of melted medium, held in a water bath at 60° to 65° C. The tubes were poured immediately, and the plates rotated to ensure thorough mixing. When cool, the plates were inoculated at a central point with mycelium of *S. laxa* from a stock culture, and incubated at 25° C. Growth of the cultures was subsequently measured along two predetermined diameters at right-angles to each other. Plate I illustrates a typical series of plates five days after inoculation.

EXPERIMENTAL.

Experiment 1.—Preliminary spore germination tests.

The test-tube dilution technique recommended by the American Phytopathological Society, Committee on Standardization of Fungicidal Tests, (1947), was used for this experiment. A series of dosages of the fungicide under test was prepared. 0.8 ml.* samples of each dilution were pipetted into small test-tubes (5 cm. by 1 cm.), and to each of these was added 0.2 ml.* of a mixture of equal parts of a spore suspension of *S. laxa* (500,000/ml.) and 1 per cent. orange juice. The final concentration of spores was thus 50,000/ml. and that of the orange juice 0.1 per cent. The concentrations of fungicide quoted in the results are also those in the final mixture.

After thorough agitation, three drops from each test-tube were pipetted out on the slides. The germination of 100 spores was recorded after incubation at 25° C. for 17 hours. ED-50 values were estimated from the provisional probit lines. Table I shows the ED-50 values obtained for each material from a single test. Bracketing of compounds indicates that they were tested simultaneously.

These results afforded some indication of the relative toxicities of the fungicides examined, and provided an effective and speedy method of selecting those obviously worthy of further trial. However, since, in general, materials were tested singly and each once only, the data can be used only as an indication of large differences in toxicity and not for more detailed comparisons between fungicides.

* Instead of 2 ml. fungicide and 0.5 ml. spore suspension, as recommended.

TABLE I.

Fungistatic ED-50 values of various fungicides against conidia of S. laxa.

Fungicide.	ED-50 value (p.p.m.)
Diphenyl mercuric salt of di-2 : 2'-naphthyl methane-3 : 3'-disulphonic acid	0.069†
Phenyl mercury acetate (90%)	0.077†
Phenyl mercury chloride	0.083†
Phenyl mercury formamide	0.053†
Phenyl mercury chloride	0.066†
Phenyl mercury monoethanol ammonium acetate	0.13 †
1-phenyl-3 : 5-dimethyl-4-nitroso-pyrazole (J.55)	0.089
1-(4-chlorophenyl)-3 : 5-dimethyl-4-nitroso-pyrazole (J.49)	0.20
× 8-Hydroxyquinoline sulphate	0.37
× 2 : 3-Dichloro-1 : 4-naphthaquinone (50%)	0.39
Sodium pentachlorophenate	0.61
Bis (2-hydroxy, 5-chlorophenyl) sulphide	0.66
Colloidal sulphur (50%)	0.71
× Standard laboratory Bordeaux mixture	0.74*
× Glyoxalidine acetates (54%) (plus lime)	0.88*
N-trichloromethylthiotetrahydrophthalimide	0.89
Malachite green	1.2
Sodium dinitro-ortho-cresolate	2.5
× Lime-sulphur	2.8
Sodium hypochlorite (expressed as free Cl)	2.9
× Copper 8-quinolinolate	4.0
Copper sulphate (pentahydrate)	8.6
Ferric dimethyldithiocarbamate	9.8
Zinc dimethyldithiocarbamate	11.0*
Dinitro-ortho-cresol (in oil emulsion)	11.0
1-(4-sulphamylphenyl)-3 : 5-dimethyl-4-nitroso-pyrazole (36-L)	38.0
Tar-oil	52.0
Sodium arsenite	79.0
Zinc ethylene bisdithiocarbamate (65%)	> 100.0
Pentachloronitrobenzene (20%)	> 100.0
Copper naphthenate (in oil emulsion)	> 100.0
JD-2 petroleum oil	> 100.0
70 total 33 Monocalcium arsenite	> 100.0

Note: † expressed as p.p.m. Hg.

* with 0.2 millimolar MgSO_4 as additional spore stimulant.

The notable features in the results quoted are the high toxicity of the mercurials and several of the newer fungicides, while copper naphthenate and the arsenites, both of which had received favourable reports in field trials by other workers, were relatively ineffective in these tests.

Apart from the materials selected for more thorough examination by means of a horizontal sprayer technique, which will be considered below, mention should be made of the high toxicity of the new fungicides N-trichloromethylthiotetrahydrophthalimide, bis (2-hydroxy, 5-chlorophenyl) sulphide, and the 4-nitroso-pyrazoles J.49 and J.55; the ED-50 value for each was below 1 p.p.m., and they show promise for further trial. While the ED-50 value for colloidal sulphur was as low as 0.71 p.p.m., it should be noted that the slope of its dosage-response curve

was unusually low, its ED-95 being 6.5 p.p.m., compared with values of less than 2 p.p.m. for the other fungicides mentioned above.

Experiment 2. Precision spore germination tests.

In this experiment the horizontal sprayer technique was used, and consequently the spores were tested against fungicide residues that had been allowed to dry on the test slides.

A general account of this experiment has already been published, together with estimates of the ED-50 values obtained from provisional probit regression lines (Byrde, 1950). Briefly, the experiment involved the testing of seven fungicides, by means of a horizontal sprayer technique, in a balanced incomplete block design; such a layout permits statistical analysis to eliminate day-to-day variations (Finney, 1947; p. 82). Each material was tested three times, and altogether seven series of tests were carried out.

The seven fungicides tested, together with their code letters, were as follows:

- A. Standard laboratory Bordeaux mixture (expressed as Cu).
- B. 8-Hydroxyquinoline sulphate.
- C. 2:3-Dichloro-1:4-naphthaquinone (50 per cent.).
- D. Phenyl mercury chloride.
- E. Lime-sulphur.
- F. Copper 8-quinolinolate.
- G. Glyoxalidine acetates (54 per cent.).

The detailed results are given in the Appendix as Tables A to C.

A summary of the results of the analysis may be expressed as follows:

SUMMARY OF RESULTS OF ANALYSIS.

Fungicide.	Corrected mean log ED-50.	Corrected mean ED-50($\mu\text{g} \cdot \text{cm}^2$)	Fungicidal value taking lime- sulphur as unity.
A. Standard laboratory Bordeaux mixture (as Cu)	2.3548	0.2263	4.01
B. 8-Hydroxyquinoline sulphate	1.7776	0.05992	14.9
C. 2:3-Dichloro-1:4-naphthaquinone (50%)	1.5019	0.03177	28.2
D. Phenyl mercury chloride	0.9062	0.008058	111.1
E. Lime-sulphur	2.9519	0.8952	1.0
F. Copper 8-quinolinolate	1.8434	0.06972	12.8
G. Glyoxalidine acetates (54%)	2.5276	0.3370	2.71

Standard error of difference between mean log ED-50 values = 0.1347. Least significant difference ($P=0.05$) = 0.3112.

The order of toxicity of the fungicides at the ED-50 level is given by the inequalities $D > C > B > F > A > G > E$ and $C > F$.

These results, which have been mathematically computed, and are each based on the results of three tests on different days, afford reliable data for detailed comparison between the seven fungicides. The high toxicity of phenyl mercury chloride and dichloronaphthaquinone is noteworthy.

It is interesting to compare these ED-50 values, expressed as $\mu\text{g} \cdot \text{cm}^2$ of dried

fungicidal deposit, with the corresponding ED-50 values shown in Table I, which are expressed as p.p.m. of fungicidal solution or suspension in which the spores were germinated. Such comparison suggests that there may be wide differences among fungicides in availability of actual toxicant from dried spray deposits. It should be stressed, however, that the data of Table I are subject to large errors.

Experiment 3. Growth rate of mycelium on agar with added toxicants.

As mentioned in the description of methods (p. 136), the mycelial growth rates of *S. laxa* on potato dextrose agar containing fungicides were estimated by measurement along two predetermined diameters of the colony at right-angles to each other. Measurements were recorded on the second, third, fourth and fifth days after inoculation; beyond the fifth day, there was a tendency for "staling" of the cultures, with a marked decrease in growth. By plotting the mean diameter (cm.) against time (days), the growth rate (cm. per day) was estimated for each colony.

Preliminary tests were carried out on a range of fungicides, using each at a concentration in the medium of 100 p.p.m. The following materials completely inhibited growth of *S. laxa*, and were tested further at lower concentrations:

Phenyl mercury chloride.

8-Hydroxyquinoline sulphate.

Sodium pentachlorophenate.

Sodium dinitro-*ortho*-cresolate.

Malachite green.

1-phenyl-3 : 5-dimethyl-4-nitroso-pyrazole (J. 55).*

The following materials permitted growth at 100 p.p.m. and were not tested further:

Copper sulphate.

Lime-sulphur.

Glyoxalidine acetates (54 per cent.).

Sodium arsenite.

2 : 3-Dichloro-1 : 4-naphthaquinone.

N-trichloromethylthiotetrahydrophthalimide.

Dinitrocaprylphenylcrotonate (25 per cent.).

The six materials which prevented mycelial growth at a concentration of 100 p.p.m. were then tested twice at a series of lower dosages. The percentage inhibition of mean growth rate, by comparison with the control value, was estimated for each concentration of fungicide. Dosage-mortality lines were fitted to these results by transformation of percentage inhibition figures to probit values and plotting these against the logarithms of the dosages. Table II shows the estimated ED-50 and ED-95 values obtained from the provisional probit lines.

Mycelial growth in media containing 8-hydroxyquinoline sulphate did not follow the usual pattern. Concentrations of approximately 2 p.p.m. and above completely inhibited growth, while below approximately 0.4 p.p.m., normal growth occurred. At concentrations within these limits, there was a long initial lag period, followed by a marked increase of growth at a rate comparable with that of control plates. As a result, it was impossible to determine a mean growth rate as had been done for the other fungicides. It was found that the addition of some metals, and particularly molybdenum, overcame the lag period, recalling the findings of Zentmyer

*From alcoholic stock solution with corresponding alcohol controls.

TABLE II.

ED-50 and ED-95 values (p.p.m.) for five fungicides against mycelial growth of S. laxa.

Fungicide.	ED-50 values (p.p.m.)		ED-95 values (p.p.m.)	
	Tests 1 and 2.	Logarithmic mean.	Tests 1 and 2.	Logarithmic mean.
Phenyl mercury chloride	{ 1.0 1.2	1.1	{ 4.8 2.6	3.5
Malachite green	{ 1.2 1.4	1.3	{ 4.9 8.0	6.2
Sodium pentachlorophenate	{ 1.55 1.2	1.4	{ 5.9 4.0	4.8
1-phenyl-3:5-dimethyl-4-nitroso- pyrazole (J.55)	{ 2.8 3.2	3.0	{ 18.6 22.3	20.4
Sodium dinitro- <i>ortho</i> -cresolate ..	{ 3.3 5.6	4.3	{ 18.6 32.0	24.6

(1943, 1944) on the antidoting of the fungistatic action of 8-hydroxyquinoline sulphate by zinc.

In these tests against the mycelium of *S. laxa*, many materials highly fungistatic to germinating spores under the test conditions were relatively ineffective against a mycelial inoculum on an agar medium. Glyoxalidine acetates (54 per cent.), lime-sulphur, 2:3-Dichloro-1:4-naphthaquinone and N-trichloromethylthiotetrahydrophthalimide fell into this category, while copper sulphate at 100 p.p.m. actually stimulated the fungus.

Of the six materials subjected to fuller testing, all showed good fungistatic properties, with phenyl mercury chloride, malachite green and sodium pentachlorophenate outstanding; these three compounds each reduced mycelial growth by 50 per cent. at concentrations of the order of 1 to 2 p.p.m. The unusual behaviour of 8-hydroxyquinoline sulphate has already been discussed.

DISCUSSION.

In subsequent papers, the results of field trials against the brown rot fungi will be compared with the laboratory data presented in this paper. At this stage, however, it may be noted that the field use of a fungicide should be taken into account in deciding which of the laboratory methods of bioassay is most likely to reflect its field performance.

For example, many fungicides are applied to leave a residue inhibiting spore germination, thus preventing infection of the plant surface beneath. For laboratory assessment of such protectant action, a spore germination test using a horizontal sprayer technique seems appropriate, and has proved its value in recent years.

The action of an eradicant fungicide differs from that of a protectant in that the material acts against fungal mycelium which is already established, and in the presence of a large quantity of the host substrate. For a laboratory assay of eradicant efficiency, therefore, the testing of the fungicide against mycelial growth in an agar medium seems more logical than a spore germination test. This has proved to be the case in the laboratory and field tests against *Sclerotinia* spp. described

in these papers. As already mentioned, several fungicides, valuable as inhibitors of conidial germination in orange juice, were comparatively ineffective against the mycelium in a potato dextrose agar medium. These same materials were subsequently found to be generally inefficient as eradicant fungicides.

The criticism of the agar method by Horsfall (1945), that the presence of organic matter interferes with fungicidal action, therefore appears less justified when evaluating eradicant fungicides, which, in fact, need to be effective in the presence of organic matter.

In conclusion, it should be stressed that fungitoxicity is only one of several factors in the performance of both protectant and eradicant fungicides: physical properties, such as tenacity in the case of protectants, and penetration in the case of eradicants, are of great importance.

SUMMARY.

1. Precision spore germination tests showed the high toxicity of phenyl mercury chloride and 2 : 3-dichloro- 1 : 4-naphthaquinone towards conidia of *Sclerotinia laxa* and *S. fructigena*. In preliminary laboratory tests, several newly-introduced fungicides showed promise, notably N-trichloromethylthiotetrahydrophthalimide, bis (2-hydroxy, 5-chlorophenyl) sulphide, and two substituted 4-nitroso-pyrazoles.

2. Laboratory tests on the effect of fungicides on the mycelial growth of *S. laxa* in potato dextrose agar showed that several materials toxic to the conidia at less than 10 p.p.m. were relatively ineffective at 100 p.p.m. against the mycelium. Phenyl mercury chloride and sodium pentachlorophenate were the most effective compounds in these mycelial tests.

APPENDIX.

TABLE A.

Dosage-mortality data of Experiment 2.

Test No.	Fungicide code.	Equation.	b (Slope).	m (Log ED-50).
1	A	$Y = 5.57x - 6.72$	5.57 ± 0.39	2.10 ± 0.01
1	B	$Y = 11.84x - 15.47$	11.84 ± 2.55	1.73 ± 0.02
1	C	$Y = 7.54x - 6.29$	7.54 ± 0.70	1.50 ± 0.01
2	A	$Y = 10.36x - 21.19$	10.36 ± 1.01	2.53 ± 0.01
2	D	$Y = 13.58x - 5.82$	13.58 ± 1.39	0.79 ± 0.01
2	E	$Y = 6.03x - 12.53$	6.03 ± 0.45	2.91 ± 0.01
3	B	$Y = 7.37x - 7.07$	7.37 ± 0.59	1.64 ± 0.01
3	D	$Y = 8.59x - 3.25$	8.59 ± 0.83	0.96 ± 0.01
3	F	$Y = 5.94x - 5.79$	5.94 ± 0.49	1.82 ± 0.01
4	A	$Y = 6.24x - 9.52$	6.24 ± 0.50	2.33 ± 0.01
4	F	$Y = 3.92x - 2.56$	3.92 ± 0.30	1.93 ± 0.02
4	G	$Y = 8.52x - 15.82$	8.52 ± 0.88	2.44 ± 0.01
5	C	$Y = 10.37x - 9.09$	10.37 ± 1.02	1.36 ± 0.01
5	D	$Y = 10.95x - 4.41$	10.95 ± 1.27	0.86 ± 0.01
5	G	$Y = 6.25x - 10.49$	6.25 ± 0.49	2.48 ± 0.01
6	B	$Y = 7.91x - 10.15$	7.91 ± 0.73	1.91 ± 0.01
6	E	$Y = 5.83x - 12.17$	5.83 ± 0.48	2.94 ± 0.01
6	G	$Y = 7.06x - 13.78$	7.06 ± 0.54	2.66 ± 0.01
7	C	$Y = 6.95x - 6.13$	6.95 ± 0.82	1.60 ± 0.01
7	E	$Y = 6.47x - 15.92$	6.47 ± 0.62	3.23 ± 0.01
7	F	$Y = 7.60x - 9.21$	7.60 ± 0.61	1.87 ± 0.01

Note: $x = \log$ deposit ($\mu\text{g} \cdot 1000 \text{ cm}^2$).

All bodies of data were tested for heterogeneity; in only one instance out of twenty-one was the value of χ^2 significant ($P=0.05$); so that evidently the results were substantially homogeneous.

TABLE B.
Incomplete Block Analysis of values of "m" from Table II.

Fungicide.	1	2	3	4	5	6	7	Totals.	Q.	v.	Corr. mean.
A ..	2.10	2.53	—	2.33	—	—	—	6.96	2.62	0.3743	2.3548
B ..	1.73	—	1.64	—	—	1.91	—	5.28	-1.42	-0.2029	1.7776
C ..	1.50	—	—	—	1.36	—	1.60	4.46	-3.35	-0.4786	1.5019
D ..	—	0.79	0.96	—	0.86	—	—	2.61	-7.52	-1.0743	0.9062
E ..	—	2.91	—	—	—	2.94	3.23	9.08	6.80	0.9714	2.9519
F ..	—	—	1.82	1.93	—	—	1.87	5.62	-0.96	-0.1371	1.8434
G ..	—	—	—	2.44	2.48	2.66	—	7.58	3.83	0.5471	2.5276
Totals ..	5.33	6.23	4.42	6.70	4.70	7.51	6.70	41.59	0	0	—

TABLE C.

Analysis of Variance of data of Table B.

Source of variance.	Degrees of Freedom.	Sums of Squares.	Mean Squares.
Tests	6	2.6414	0.4402
Fungicides	6	6.5949	1.0991
Error	8	0.1694	0.02117
Total ..	20	9.4057	

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PLATE I.

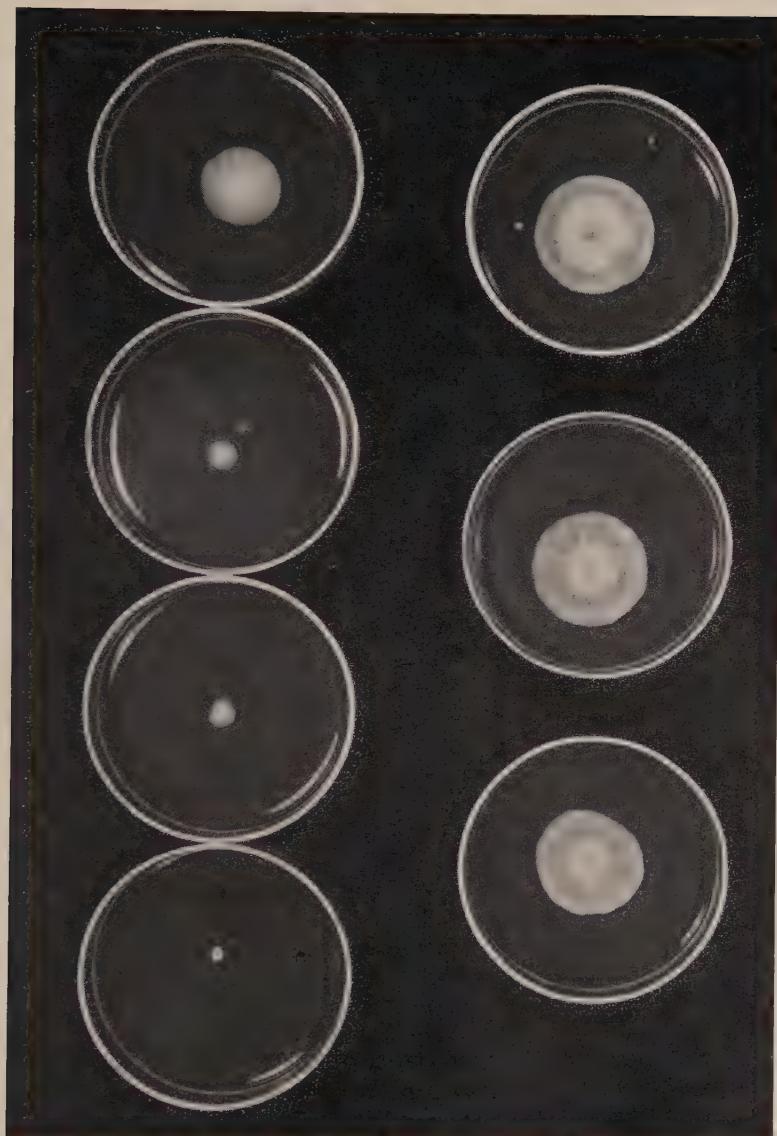


FIG. 2.

A series of plates showing growth of *S. laxa* five days after inoculation on a medium to which have been added various concentrations of 1-phenyl-3 : 5-dimethyl-4-nitroso-pyrazole (J.55).
Top row, left to right : 16, 8, 4, 2 p.p.m.
Bottom row, left to right : 1, 0.5 p.p.m., control.

REVIEWS

MITTEILUNGEN. Edited by J. KRAUS. (Klosterneuburg: Vol. I, No. 1. January, 1951. Pp. 44.)

Mitteilungen (Communications) is the title of a new Austrian horticultural journal issued by the "Höheren Bundeslehr- und Versuchsanstalt für Wein-, Obst- und Gartenbau Klosterneuburg" (The Higher Education and Research Institute for Viticulture, Fruit-growing and Gardening, at Klosterneuburg, a few miles north of Vienna). The Editor attaches great importance to the international exchange of views, and foreign scientists and horticulturists are invited to contribute reports on their work. The current number includes articles on the application of growth substances in raising grape vines, on cold storage of fruit and on subsoil irrigation.

H.W.

BETTER ROSES. By A. S. THOMAS. (Sydney and London: Angus and Robertson, 48 Bloomsbury Street, W.C.1. 1950. Pp. 295, illus. Price 19s. 6d.)

When I first read this book, it was rather a hurried perusal but, studying it now for the second time, I am the better able to appreciate it as a most noteworthy book on the Rose. The different conditions prevailing in the vast continent of Australia for the cultivation of the Queen of Flowers is catered for in a knowledgeable and comprehensive manner, and all rosarians "down under" should read it. For the English reader there is also much of interest, particularly in the more scientific aspects of the subject which are universal.

One must get accustomed, however, to the fact that "facing north" means *into* the sun, that their winter means our summer and that spring is in September. In many parts of the continent there are two full flushes of flowering in April, May and again in October, with periods of rest in between; in other parts roses may bloom all the year round. The climate nearly everywhere appears to be much more favourable to the rose than is ours and their problems are very different. The growth of their trees is much stronger than we are familiar with, and much lighter pruning can be practised than is usually possible in this country.

Dr. Thomas is a scientist and the chapters on hybridization, chemistry of the soil, fertilizers, etc., are dealt with in a way that only a scientist could, yet clearly and simply for the ordinary gardener, both in Australia and in England.

The varieties grown are mostly the same as with us but, in addition, many are grown, such as the descendants of *R. gigantea*, which would not be hardy enough to withstand our winters. Loraine Lee is said to be one of the most popular varieties there, but this and many other home-produced roses are unknown to me. Golden Dawn is the only one that has come to us from Australia, but surely there must be many more, worthy enough for introduction here. I do not know why Dame Edith Helen is classed as a Pernetiana. It may have some slight strain of *R. foetida*, but most modern roses have, and Dame Edith has less than most. It is interesting to know that this is one of their best exhibition varieties; the English strain, however, has deteriorated to such an extent that it is becoming practically obsolete.

I am sorry that the author perpetuates the term "Austrian Briar". *R. foetida* was grown in England in the sixteenth century and it was not until William Paul in 1848 used this false name that it became current. Paul erroneously stated that it was a native of Germany, Italy and France; anyway it never had anything to do with Austria, except that it was cultivated in gardens there. It is a native of South-west Asia.

On the subject of rose nomenclature, Dr. Thomas is a purist but he does not quite appreciate the practical difficulties on this side of the world and the many contradictions and inconsistencies in the "rules" for naming new varieties. For instance, which rule is to have precedence, that no name shall be changed from its country of origin, or that no name shall be used that has been used before? (*vide* Caprice). I would also remind the author that patent rights are available for new varieties in France as well as in America.

This book is profusely illustrated both with colour plates and in monochrome, and it should be specially noted that all profits from the sale of the book—and it should have very good sales—are generously to be donated to the National Rose Societies of Australia and New Zealand.

B.P.

PESCHICOLTURA (PEACH GROWING). By N. BREVIGLIERI. (Trattati di Agricoltura, Vol. II. Ramo editoriale degli Agricoltori, Rome. 1950. Pp. 590, illus. Price 3,000 lire.)

This book, a valuable addition to our knowledge of peaches and peach-growing in the open, is compiled by a professor of fruit-growing at the University of Florence. It is the first of its kind published in Italy and so fills a gap in the horticultural literature of that country. The story of peach-growing in Italy is lost in the "night of time", but it is only in the last fifty years that peaches have become important enough for their cultivation to be one of the chief national industries.

Two important works on peaches are Hedrick's *The Peaches of New York*, 1917, illustrated by many magnificent plates, and a recent monograph by Caillavet and Souty. These, however, are chiefly devoted to nomenclature and descriptions of varieties, while the Italian book confines varietal descriptions to one chapter and pays detailed attention to other aspects of peaches and peach-growing. Its twenty-five chapters contain historical data (particularly the early history of the peach in Italy); classification with botanical and pomological descriptions; genetics and the improvement brought about in various countries by breeding; sexual reproduction and propagation by clones; rootstocks and compatibility; descriptions of varieties (chapter 10, pp. 165-219 with many photographs and two coloured plates); cultural operations (budding, manuring, irrigation, pruning, thinning the fruits); costs of production; parasites and diseases; harvesting the crop; storage; drying and canning. Numerous references appear as footnotes on the relevant pages, and indexes are supplied of both authors and varieties.

The book is fully illustrated throughout and its general appearance is attractive. The paper binding, however, is insufficient for a work of this size and quality. The author himself has written many original articles on various aspects of peach-growing and it is evident that he has made a careful and detailed study of his subject. The book is one to be consulted by all who are interested in out-door peach cultivation.

H.W.

ECONOMICS OF A FRUIT FARM. By R. R. W. FOLLEY. (London: Oxford University Press. 1951. Pp. 103. Price 12s. 6d.)

This book sets out in economic terms the development of a fruit farm from planting to the sixteenth year. The first phase, or establishment of the orchards, is taken as the time from planting to the first year when annual revenue exceeds expenditure. This occurred in the seventh year and, but for a frost, would have occurred in the sixth year. The accumulated cost over this period of about £100 per acre (excluding cost of land), agrees with other published information for this period (1932-39). Tables are given showing how this money was spent, providing useful data for the prospective fruit-grower budgeting for the future, especially when considered in conjunction with the information given on how the venture was financed.

Income in the early years is analysed and the importance of quality production and grading is shown in economic terms which is not without its application now. The part played by the cordons in providing income in the early years is significant.

What is of particular interest to all fruit-growers is the second phase of readjustment and reconstruction. The dessert apple trees were planted mainly on a 12 ft. by 12 ft. plan with a balance of 68.7 per cent. dessert to 31.3 per cent. culinary. An extensive programme of grubbing and top grafting was undertaken to reduce the number of trees and amend the balance of varieties to 93.9 per cent. dessert and 6.1 per cent. late culinary.

It is concluded that the original policy of close planting in this case was correct. The effect of tree grubbing on cropping and financial returns is stated and this kind of information is, so far as I am aware, not available elsewhere. A complicated process is commendably simplified by the author and interesting comparisons are drawn.

Fruit trees are a permanent crop, but the progressive grower has to be alive to changing needs and practices. Although the story of the development of this farm is told in economic terms only (there are no illustrations other than graphs), it nevertheless reveals intense application to improve production and to achieve the success ultimately derived.

O.G.D.

ANNUALS FOR GARDEN AND GREENHOUSE. By J. S. Dakers. (London: W. H. and L. Collingridge Limited. 1951. Pp. 140, illus. Price 8s. 6d.)

This book is dedicated to the amateur gardeners of England and among these must surely be accounted many whose profession is horticultural science. For this reason and because, after all, the hardy annuals are among the easiest to grow and most rewarding of all summer flowers to those whose gardening hours are limited, we draw attention to Mr. Dakers' book. If it is valued for nothing more, it is worth possessing for its descriptions of more than one hundred different kinds and the reviewer will certainly consult it when he prepares his seed list for next year's annual border.

T.N.H.

THE CLEMATIS. By ERNEST MARKHAM. (London: "Country Life." 1951. Pp. 120, illus. Price 18s.)

This book *The Clematis*, by Ernest Markham, edited by that knowledgeable plantsman, A. G. L. Hellyer, is the third edition since the first was published in 1935,

the second being brought out in 1939. All three editions have been "Country Life" publications. In this new edition a great number of the plates have been changed, and the more modern production of these is an advantage as they are much clearer than those in the first edition. The only thing they lack is colour for, as the dust cover shows, the colour of these plants can be glorious in certain varieties.

There is a useful chapter on the history of the clematis but, unfortunately for the student, the tropical clematis and all those which need glasshouse treatment have been ignored; otherwise it would have been a more valuable work on this fascinating subject. There is also a useful chapter dealing with the use of the clematis in the garden which suggests species and varieties which do best in certain places, but it would have been easier if the Editor had stated which types he referred to as large-flowered hybrids. The chapter on propagation is extremely valuable, and it is interesting to discover that cuttings root freely, some with and some without heat. Vegetative propagation produces a plant which is less liable than grafted plants to that terrible scourge, wilt.

A very useful chapter now included, and which does not appear in the first edition, is the one on planting. Anyone interested in plant hybridization will be spurred on to try his skill at this when he realizes on reading Chapter 5 the ease with which it may be accomplished. The chapter dealing with the clematis as a cut flower is well worth noting, especially as it mentions that part of the old wood should be cut, whereas many flowers take up water only through the younger wood. It is also interesting to learn that in Holland some varieties are used for commercial cut flowers. The chapter also includes a list of varieties which may be used in this way. The chapter on pests and diseases holds out some hope for the anxious gardener, as it suggests remedies for most of those which worry the grower of these beautiful plants. A welcome addition is the chapter which explains pruning, a frequent cause of failure with amateurs, who are forgetful whether the plant flowers on new wood or old and who cut away all wood indiscriminately. The chapter which describes species and hybrids and lists varieties under their appropriate parent plant is very helpful.

Useful for the professional and amateur gardener alike are the lists of clematis for the large and small garden, the species which are worth growing and the best of the herbaceous types. The book also contains a well compiled index. This is a publication which all lovers of the clematis should obtain, especially if they do not already possess earlier editions.

M.P.

THE ASSOCIATION OF ANTS WITH APHIDS AND COCCIDS. By G. E. J. NIXON. (London: Commonwealth Institute of Entomology. 1951. Pp. 36. Price 5s. net.)

In this review, the author has considered every aspect of the association of ants with aphids and coccids. The survey on the subject covers the literature up to the end of 1948. For convenience the paper has been divided into several main headings devoted to the various aspects of the problem. They are as follows: the nature of the association; the ants that attend aphids and coccids; the advantages of the association to aphids and coccids; the effect of the association on the host-plants and the economic significance of the association. In addition there is a brief but clear introduction, and the work is terminated by a number of

reasoned conclusions which adequately sum up the varying aspects of the subject and will be of particular interest to the economic entomologist.

The review stresses very clearly that the theories of many writers, advanced from time to time to explain the behaviour of ants to aphids and coccids, need to be considerably modified. For example, the part ants play in the transportation and dissemination of aphids and coccids, at one time generally accepted, is now open to doubt. Also the amount of protection afforded to aphids and coccids by the ants driving away parasites and predators appears to be very limited.

The old and very attractive belief that ants behave towards aphids and coccids as though they were "cattle" has also to be abandoned, and when discussing the fascinating problem one can do no better than to quote direct from the author: "Whatever may be the true nature of the diverse relations between ants and Homoptera, it is certain that to understand them, the old subjective and picturesque interpretation that ants behave towards aphids and coccids as though they were 'cattle', requiring to be 'milked' and otherwise tended, must be abandoned."

A detailed account is also given concerning the association of ants with aphids and coccids, with special reference to the part played by the ants where the association is believed to be connected with the transmission of virus diseases.

Finally, there is a bibliography consisting of some four hundred references relevant to the subject, and an index to the scientific names of the insects referred to.

A.M.M.

SOIL CONDITIONS AND PLANT GROWTH (8th Edition). By SIR E. JOHN RUSSELL. Revised by E. W. Russell. (Longmans, Green. 1950. Pp. 634, illus. Price 35s.)

Sir E. John Russell's *Soil Conditions and Plant Growth* first appeared in 1912 and, in the form of its various editions up to the seventh in 1937, has been accepted as the standard textbook on the subject. Soil scientists have eagerly awaited the publication of this eighth edition, revised by Dr. E. W. Russell, son of the original author. The revision has been thorough, in fact all except the first chapter (Historical and Introductory) has been recast and rewritten. This has involved the study of an enormous amount of literature covering all the diverse aspects of the subject, and the presentation of the whole in a readable form. This prodigious task has been brilliantly carried out and the result is a book which will be indispensable to all who are interested in the way in which the growth of plants is affected by the soil. The examples quoted mostly concern agricultural rather than horticultural crops but the book is no less valuable to the horticultural worker on that account, for the general principles are the same.

After the historical introduction, three chapters are devoted to the nutrient requirements of plants, including a consideration of each of the essential elements in turn and a section on the interaction of nutrients. The composition and properties of the soil are dealt with in chapters 5-8, including sections on pH and on the effects of fertilizers on the soil.

Next follows a long section on soil biology which covers the whole field from bacteria to earthworms and even mammals, including excellent discussions on the physiology of the microbial population, on soil ecology and on associations between plants and micro-organisms. This leads naturally to a chapter on the decomposition of plant material, including a useful discussion of green manuring, and hence to the

subject of the composition of soil organic matter. A comprehensive account of the nitrogen cycle, containing a section on the importance of leguminous plants, occupies the longest chapter in the book.

With chapter 17, the subject changes abruptly to soil physics. Soil temperature is briefly but adequately dealt with, but one could wish that it had been possible to give a more detailed discussion of the soil atmosphere. On the other hand, the four chapters on soil moisture cover the subject fully and provide a most useful account of the modern interpretation of water relationships of soils and plants. The physics section ends with an interesting chapter on soil structure, including the effects of cultivations and of growing crops and the mechanism of crumb and clod formation.

The theme changes again in chapter 24, which concerns the development of plant roots and includes references to root studies on fruit trees. Following naturally from this are chapters devoted to the uptake of nutrients and water by the roots, to the sources of nutrients in the soil, and to the effect of pH on plant growth. Then, turning from the effect of soil conditions on plant growth, chapter 28 is concerned with the opposite effect, that of the plant on the soil. The uses of leys are discussed, and a section on the interaction between plants growing together leads to a mention of the reasons for cover cropping in orchards.

Soil formation is dealt with in chapters 29-31, and the next two chapters are devoted to saline and alkali soils and their management. Chapter 34 is entitled "The General Principles of Soil Management" but, after a brief introduction, deals solely with erosion control, the other aspects of soil management being discussed in the next two chapters. Thus, chapter 35 deals with methods of soil cultivation and includes a section on mulches and shade-trees. The effects of mulches are of particular interest to fruit-growers, but there is no mention of the non-cultivation system of soil management involving the use of weed killing sprays, which is being widely used in Californian citrus plantations. The final chapter summarises the essential conditions for fertility, and discusses the soil management methods necessary for maintaining fertility in different types of soil. The last section of this chapter, on the principles of land classification, seems out of place.

The book is easy to read, though there are a few grammatical idiosyncrasies which will doubtless annoy the purist. For a book of this size, there are comparatively few errors, including about a dozen obvious misprints which do not affect the meaning. But it should be noted that the reference half-way down p. 18 should be to p. 14, not to p. 12, and that on p. 398 the plate referred to is XVII, not XXII. The caption to Plate II appears to be incorrect as the result of an error in punctuation, while on p. 570, line 1, "finer" should surely read "coarser". But these are minor blemishes. A more serious defect is that one cannot always find what one wants by using the index. There is no separate bibliography, but the author index refers to pages on which the very large number of references are given as footnotes. This method of giving references, using small index numbers in the text, is quite the most convenient for the reader.

The thirty-eight plates are good, and both these and the figures have been well chosen to illustrate the text. The general appearance of the book is so attractive that anyone interested in the effects of soil conditions on plants will have the greatest difficulty in resisting the temptation to buy it. Those who succumb to the temptation will have no regrets.

D.W.P.G.

THE BIOLOGY OF THE STRAWBERRY APHID, *PENTATRICHOPUS FRAGAEFOLII* (COCK.), WITH SPECIAL REFERENCE TO THE WINGED FORM

By G. H. L. DICKER
East Malling Research Station, Kent

SINCE Harris (1933, 1937) demonstrated the presence of yellow-edge and crinkle viruses in the cultivated strawberry in this country, these diseases have assumed an increasingly important role until, at the present day, they are considered to be mainly responsible for the degeneration which so often occurs in commercial beds (Whitehead and Wood, 1946). As far as is known, the viruses can be spread only by propagating from diseased stock or by means of an insect vector. Massee (1935, 1942) showed that the Strawberry Aphid, *Pentatrichopus fragaefolii* (Cock.), transmitted both virus diseases, but Rogers, King and Massee (1939) failed to get transmission with "other species of strawberry aphids, a white fly, a species of leaf hopper, the strawberry tarsonemid mite and the red spider mite". Whitehead and Wood tested, with negative results, five species of aphids found infesting commercial strawberries; they did, however, transmit crinkle with *Pentatrichopus tetrarhodus* (Walk.), an uncommon species which normally lives on rose and is known only to colonize strawberries under artificial conditions, and, from the results of their own experiments and those of Massee (1936, 1937), they concluded that *P. fragaefolii* could transmit virus in all months of the year. Prentice and Harris (1946) and Prentice (1948, 1949) have shown that the diseases as originally described contain at least three distinct viruses which can be separated by means of this aphid vector. The Strawberry Aphid is thus shown to be capable of transmitting all the virus diseases known to occur in the cultivated strawberry in this country and, furthermore, there is strong evidence that it is the only natural vector in the field.

In recent years, under a scheme sponsored by the Ministry of Agriculture, considerable reduction in infection during propagation has been achieved by raising runners in isolation and carefully roguing for virus at intervals during the growing season. Even under these conditions, which include the elimination of all aphids at the time of planting by dipping runners in a nicotine solution, it is found that beds have usually become infested with the Strawberry Aphid by the early summer months. This can only occur naturally by alate viviparae arriving from other strawberries and colonizing the clean plants. Both virus-infected and healthy aphids may arrive, the former being a direct menace since they are liable to transmit the virus to plants on which they feed, whilst the latter aid the spread of any virus already present by providing a vector.

It will be seen, therefore, that propagation of virus-free runners, whilst improving the general health of stocks, will not in itself eliminate the risk of infection, and control of the vector will also be essential. This is especially so of strawberries grown for fruiting, because in this country the strawberry industry is concentrated

in compact areas where the danger of infection is much greater than where runners are raised in comparative isolation.

The present investigation deals mainly with the alate viviparous form as it is the most important agent, both directly and indirectly, in spreading the virus diseases. Previous workers had noted alatae between May and July and again in the autumn, but there was no detailed information concerning either the number produced or the period over which they matured. Whilst Greenslade (1941) considered the spring dispersal period usually lasted only a week or ten days in Kent, Thomas and Jacob (1940) and Wood (1950) found it continued for six weeks in North Wales. Still less was known about alatae produced in the autumn. Field observations had already demonstrated the importance of the spring alatae in spreading virus from field to field and Greenslade showed that these forms could even find and colonize individual strawberry plants. Similar forms occurring during the autumn were considered of relatively minor importance due to the smaller numbers produced and the limitations imposed on flight by unfavourable climatic conditions.

Past workers have described the dissemination of alate viviparae from field to field as migration, a term which, though strictly correct, is very misleading for, in connection with aphids, it generally implies an obligate movement from a winter to a summer host or *vice versa*. No such thing happens with the Strawberry Aphid which lives on the same host plant throughout the year; therefore, in this paper, the term "dispersal" will be used to describe the spread of alate viviparae.

METHODS.

Sampling technique.

Population counts were made at ten to fourteen day intervals, the shortest being at periods when populations varied most. The method used was that devised by Greenslade and Pearce (1940) whereby a partly opened leaf was taken as the sample unit and the total number of aphids thereon recorded. Throughout this investigation, in addition to the total, the number of last instar nymphs possessing wing buds, and alatae, were noted separately. Between fifty and sixty samples were taken from each field, evenly distributed over the whole area where this did not exceed one acre; in larger fields approximately one acre was sampled. The first sample leaf was taken from a plant near the end of a row towards the edge of the field; further samples were taken at regular intervals along the same row until the end was reached and then back along another row and so on to the other side of the field, keeping the same interval between sample rows. The intervals between sampled plants in a row and between sampled rows were approximately equal. The actual spacing, depending on the size of the field, was calculated beforehand to give slightly more than fifty samples.

Choice of fields.

The Strawberry Aphid was kept under observation in Kent, on both Research Station plots and commercial plantings, throughout the year and other areas were visited regularly during the spring dispersal phase. Sufficient information was already available to indicate that alatae should occur during May or June. At the beginning of this investigation, in 1943, it was planned to visit Hampshire, Worcestershire and the Isle of Ely early in May and to select, with the help of local

horticultural officers, a few fields where aphids were sufficiently numerous to give satisfactory sampling results if winged forms developed later. However, alatae appeared earlier than was anticipated and the preliminary visit coincided with the appearance of the first winged forms. It should be emphasized that for this investigation it was important to sample plants carrying high populations and the fields chosen were, therefore, the most heavily infested and were not representative of the districts as a whole. On the other hand, as most alatae originated from these heavily infested fields, the results give a true picture of the production of winged forms. The number of fields sampled in each area was restricted by the time available, for all areas were visited within a period of four days. The exact location of each sampled field has not been indicated on the graphs (Figs. 5-12). Those in Hampshire were situated in the Botley and Titchfield districts; in Worcestershire at Evesham, Harvington, Pebworth, Pershore and Whittington; in the Isle of Ely at Wisbech St. Mary, Leverington, Friday Bridge, Elm and Outwell Basin; in Kent at Barming, Watlington, Comp and East Malling, collectively termed the Malling district on the graphs, and, in 1944, fields were also sampled at Westerham.

As Huxley and Royal Sovereign are the most widely grown varieties in this country both were sampled whenever suitable fields were available. This was possible except in the Isle of Ely where Huxley is practically the only variety grown. On the graphs a continuous line has been used to illustrate population curves for Huxley and a broken line for Royal Sovereign; the age of the plants is given in the key.

Estimation of alatae.

As it is impossible to know whether a winged aphid has matured on the plant where found or has arrived from another source, the numbers of last instar nymphs with wing buds were used as an estimate of alatae present. Breeding experiments showed that this instar lasted 4-7 (averaging 5.3) days during May and June and 13-16 (averaging 14.3) days in November. Samples taken at ten day intervals would thus exclude the possibility of any winged nymph occurring in two consecutive population counts during the spring dispersal period, though this may have happened occasionally in the autumn when the interval between samples was usually fourteen days. The only disadvantage of this method is that it anticipates by a few days the numbers of alatae actually produced. On the other hand it has given much valuable information, concerning both the numbers of alatae produced and their behaviour, which would not have been obtained had only alatae been recorded.

SYNONYMY AND MORPHOLOGY.

The synonymy of this species has been discussed in detail by Thomas and Jacob (1941). These workers concluded that two species of *Pentatrichopus* probably existed in North America, one of which may be identical with Theobald's *fragariae*, but a further detailed examination of type specimens would be necessary before it could be decided whether *fragariae* Theobald and *fragaefolii* Cockerell were identical or different species. Dr. Hille Ris Lambers informs the author that this has now been done and, Cockerell's species having been found to be identical with Theobald's, the Strawberry Aphid thus becomes *P. fragaefolii* (Cock.) with *fragariae* Theo. as a synonym (Thomas, 1948).

Detailed morphological descriptions of all stages except the alate male are given by Thomas and Jacob (1941).

LIFE HISTORY.

Apterous viviparae are found throughout the year on cultivated strawberries and asexual reproduction continues without interruption except at very low temperatures. Aphids normally live on the undersides of the leaves, close to one of the veins from which they feed, and show a marked preference for the younger leaves. During the spring, when populations are greatest, the colonies may extend down the stalks of young leaves and also infest the flower trusses, some being found on the sepals of maturing fruits. When the plant is in active growth there is a constant movement from the maturing leaves to the younger ones, also along the stolons to the growing tip. As a rule aphids tend to leave a leaf as soon as the leaflets have unfolded and wander down the stalk to colonize a younger leaf appearing through the crown; at the same time colonies of considerable size may

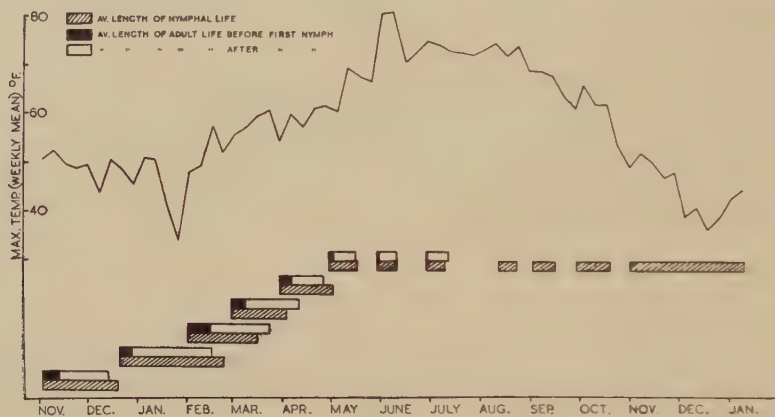


FIG. 1.

Length of nymphal and adult life at intervals throughout the year, showing relationship with the maximum daily temperature.

occur on older leaves. Where aphids have been under observation on potted plants the greatest loss of apterae occurs as each leaf matures; the aphids presumably fail to find a young leaf even if one is present and wander off the plant. It is probable that the same occurs in the field and is responsible for the spread of many apterae and nymphs to neighbouring plants. Overcrowding and disturbance by cultivation, heavy rain, strong winds and human interference with the plant also aid the plant-to-plant spread.

The length of life of both the nymph and the adult is illustrated in Tables I and II and Fig. 1. These data were obtained in a gauze insectary, with a glass roof and ventilation along the ridge, where the temperature varied only slightly from that outside. Freshly deposited nymphs were obtained by placing a number of apterous viviparous females on potted Royal Sovereign plants which were inspected daily and the adults removed as soon as nymphs were present. Up to five nymphs were allowed on each plant and normally ten to fifteen nymphs were used for observation each month. Mortality was very low except in the experiments starting in November and December, and very little variation in the length of nymphal life occurred among individuals of each monthly batch. As will be seen from Table I

TABLE I.
Length of nymphal life under insectary conditions.

Date deposited.	No. matured.	Av. time to reach maturity (days).	Date deposited.	No. matured.	Av. time to reach maturity (days).
1949			1st May	12	18.2
4th-6th November	4	47.0	31st May	10	11.7
19th-21st December	6	64.3	29th June	11	11.6
1950			13th August	13	11.0
2nd-8th February	9	43.4	2nd September	10	14.0
1st-3rd March ..	10	33.9	29th September ..	17	21.1
30th March ..	10	33.3	2nd-3rd November	5	69.8

the duration of the nymphal instars progressively decreased from December to May, remained relatively constant during June, July and August, then increased as autumn approached. Comparison with the maximum daily temperature averaged over weekly periods from thermograph records (Fig. 1) shows that, as suggested by Smith (1937), temperature is an important factor in determining the length of nymphal life. Besides a direct effect on the insect there is probably also an indirect one caused by temperature affecting the growth rate of the host plant.

Information on the length of life of the apterous viviparous female was obtained by methods similar to those described above, fourth instar nymphs being collected on a stock plant and adults, as they matured, transferred to other potted strawberries, two or three aphids being placed on each plant. To minimize the risk of contamination, each pot was placed upon a wooden block in the centre of a dish filled with water. Ten aphids were used each month, any nymphs present being removed daily. Since the adults were allowed to live freely on the plants, individuals occasionally wandered from the host and were lost before death occurred. On the other hand the sheltered insectary conditions most probably prolonged life beyond that normally to be expected in the field. Table II shows that both the length of adult life and the interval between the final moult and the appearance of the first nymph decreased

TABLE II.
Length of life and fecundity of apterous viviparous females under insectary conditions.

Date matured.	Av. no. of days before first nymph deposited.	Av. length of adult life (days).	Av. no. of nymphs per aphid.
1949			
31st October-4th November ..	10.0	40.8	14.6
21st-24th December	7.2	57.5	21.1
1950			
1st-3rd February	14.4	50.9	18.2
3rd-6th March	8.8	42.2	17.4
28th March-3rd April	7.6	26.8	13.7
29th April-1st May	3.4	17.0	20.2
2nd-3rd June	2.0	12.5	25.0
29th June	1.2	14.0	23.4

from February to June and that, in addition to a higher rate of reproduction in summer, there is an indication that more nymphs may be produced by each female.

It will be noticed that, for aphids maturing on 21st-24th December, the interval before the first nymph appeared was less than for either the November or February batches. These were brought into the laboratory as last instar nymphs and remained at a temperature of about 60° F. for two or three days until mature; they were then returned to the insectary. Further experiments have shown that the interval before reproduction starts is influenced by the temperature at which nymphs are reared.

Considerable variation occurred both in the length of adult life and the number of nymphs produced. The most long-lived aphid matured on 23rd December and died 97 days later; the most prolific were two maturing on 3rd June and living respectively for 20 and 23 days which together produced a total of 96 nymphs. Where detailed observations were made, all nymphs moulted four times, not three as observed by Masee, Greenslade and Duarte (1938). From Fig. 1 it is calculated that fourteen or eight generations would have been passed through in a year under the prevailing insectary conditions depending on whether the first or last nymph produced by each female is considered.

No information is available on the threshold temperature below which nymphs are not produced. The period of lowest temperatures when apterae were observed to breed occurred in 1950, when two adults respectively deposited a nymph on 12th and 15th December and subsequently on 28th December. During this period the temperature exceeded 40° F. for four hours only and varied from 45° F. to 27° F. with a mean, averaged over two-hour periods from thermograph records, of 33.3° F. and 33.5° F. for the periods 12th-28th and 15th-28th December respectively. Observations made during breeding experiments suggest that development of the embryo within the aphid continues even when the temperature approaches freezing point but a rise to over 40° F. is usually necessary before nymphs are deposited.

The severe winters of 1939-40 and 1946-47 resulted in very high mortality in the field. Individual aphids survived only on very sheltered plants, mainly on vigorous varieties such as Huxley where a denser canopy of foliage provided additional protection from frost. In very localized areas populations returned to normal by the autumn and from these foci *alatae* dispersed in the following spring. By 1943 and 1949 heavy infestations were again general in all districts. Recovery from the effects of the 1939-40 winter was retarded by one year compared with 1946-47 due to unfavourable, though less severe, climatic conditions in 1940-41.

Minimum screen temperatures recorded at East Malling during the coldest periods of 1939-40 and 1946-47 are shown in Fig. 2. These were chosen in preference to the grass minima as they approximate more closely to the conditions prevailing beneath the shelter of strawberry leaves. That mortality was due to low temperature there is no doubt, but the actual mechanism is less clear. For short periods the temperature may have dropped below the lethal limit for the aphid, as 2° F. was recorded on 19th January, 1940, 0° F. on 28th and 29th January, 1947 and 1° F. on 23rd February, 1947. Alternatively, the cumulative effect of prolonged periods of low temperature may well have been more important, for the minimum did not once rise above freezing point between 10th January and 4th February, 1940 and only twice between 18th January and 10th March, 1947. During most of these

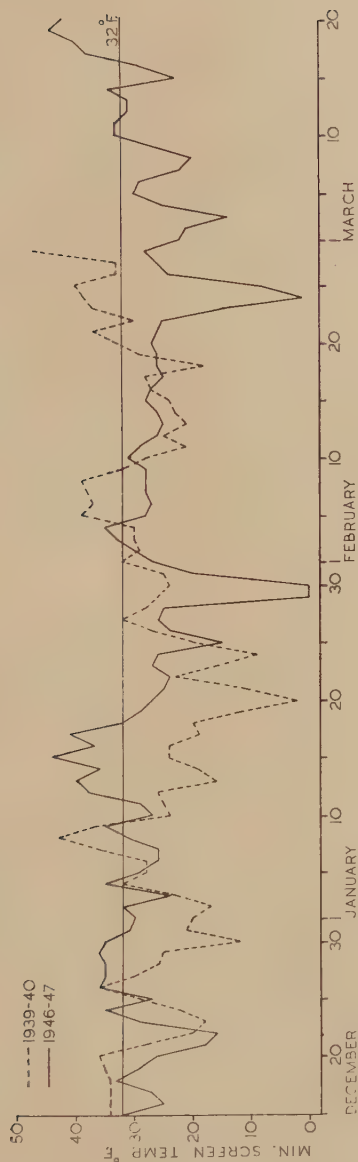


FIG. 2.

Minimum screen temperatures, December-March, 1939-40, 1946-47.

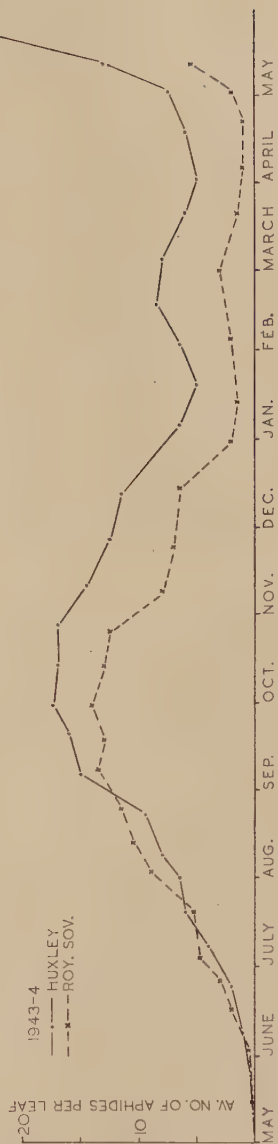


FIG. 3.

Typical population curves for the Strawberry Aphid on first-year plants which have been dipped in nicotine before planting.

periods the plants also remained frozen during the day and possibly aphids were unable to feed and died from starvation.

The reverse effect is sometimes noticed following mild winters such as 1948-49, when a more rapid rate of reproduction in the early months of the year leads to very heavy infestations by May or early June.

Under laboratory and insectary conditions, sexual forms occur fairly freely from October to January, occasional specimens having been found as late as May. Hodson (1937) and Thomas and Jacob (1940) obtained apterous males and oviparous females, whilst the writer has bred these forms and also alate males from a single clone. In the field, sexuales occur very rarely; Thomas and Jacob (1940) record one oviparous female and the writer has observed single specimens of the oviparous female and the alate male. The egg stage has never been recognized with certainty in the field and appears to be of no importance in the economy of this species—in fact it is very doubtful whether, under natural conditions, sexual forms are ever present in sufficient numbers for mating to take place. Eggs can be obtained in the laboratory but only Hodson has succeeded in breeding fundatrices; on all other occasions eggs have failed to hatch. Measurements of eggs obtained by the writer agree very closely with those quoted by Hodson; the egg described by Massee, Greenslade and Duarte (1938) is much larger and probably belongs to another species. It would appear that this species, living on an evergreen plant which provides a continuous source of food throughout the year, has gradually dispensed with the egg stage and adapted itself to a life of continuous asexual reproduction.

HOST PLANTS.

All available evidence suggests that *P. fragaefolii* has no important natural host other than the cultivated strawberry. Massee, Greenslade and Duarte (1938) and Thomas and Jacob (1940) found it on *Potentilla anserina* L. and Greenslade (1941) reported colonies on *Fragaria vesca* L. growing in cultivated ground. Twice at East Malling, in July, 1948 and in February, 1950, small colonies of apterae have been discovered on *F. vesca* growing naturally in woodland clearings, but this appears to be exceptional for, in addition to the absence of further records, there is no authenticated report of this host ever being discovered in its natural habitat with symptoms of virus, yet it is extremely sensitive when used in the greenhouse. Several plants have proved acceptable hosts under artificial conditions; Massee (1935a) induced it to breed on *Fragaria vesca*, *Potentilla anserina* and *P. sterilis* Garcke; Thomas and Jacob (1940) list also *Fragaria moschata* Duch. and *Rosa rugosa* Thunb., and Whitehead and Wood (1946) list *Potentilla comarum* Nestl. Neither Hodson (1937) nor Massee (1935a) could establish aphids on *Centranthus ruber* DC. quoted as a host by Davidson (1925). Greenslade's interesting observations that *P. fragaefolii* will establish colonies on plants of *F. vesca* growing in cultivated ground, but not when part of the normal woodland flora, still await a satisfactory explanation.

Though only a few of the well-known varieties of cultivated strawberry have received detailed attention, a marked varietal difference in the intensity of infestation has been noticed. Huxley normally carries the highest populations, followed by Royal Sovereign, Paxton and Early Cambridge; Tardive de Leopold and Perle de Prague have never been noted with more than moderate populations and Madame Lefebvre is usually only lightly infested. Preliminary observations

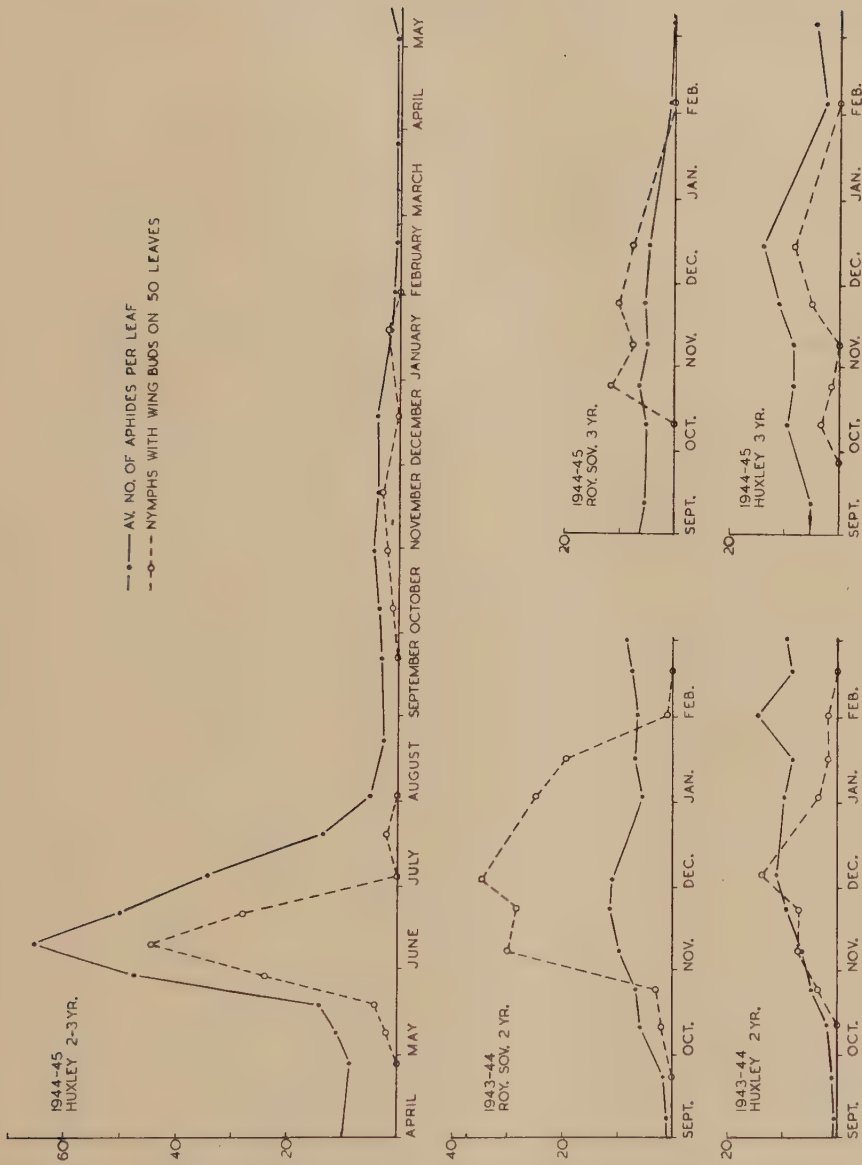


FIG. 4.

Top. Typical population curve for the Strawberry Aphid on plants over one year old.

Middle and bottom left hand. Greatest number of nymphs with wingbuds observed during the winter months on two-year-old plants,

Middle and bottom right hand. Greatest number of nymphs with wingbuds observed during the winter months on three-year-old plants,

and reports indicate that the recently introduced variety, Auchincruive Climax, is seldom heavily infested. Occasionally populations are sufficiently high in late May and early June to cause direct mechanical injury; more usually, however, damage is confined to a reduction in quality of the fruit by the growth of sooty moulds on the honey dew.

FLUCTUATIONS IN POPULATION.

On plants in their first year the initial infestation is always low and, if runners are dipped in a 0.05 per cent. nicotine solution before planting, no aphids will be present until alate viviparae arrive in May or June. Populations then build up slowly, reaching a peak in late summer or early autumn (Fig. 3). The late peak can be related to the vegetative habit of first-year plants which continue to produce a regular supply of fresh leaves throughout the summer, there being no marked reduction at fruiting time as with older plants. The decline is doubtless associated with lower temperatures influencing the rate of reproduction and plant growth.

As illustrated in Fig. 4 a different population rhythm occurs on plants over one year of age. The top graph is typical of many obtained during the period 1943-46, all of which showed the same trend though the number of aphids observed at the peak period varied greatly. Starting with a relatively low population in January, numbers remained fairly constant until late April when an increase, often very rapid, occurred, culminating in a peak during the first half of June. An equally rapid decline followed and low populations persisted for the rest of the year. A rise between October and December is often indicated by the counts, but this is contrary to detailed biological observations and is caused by a defect in the sampling technique due to seasonal variations in the growth rate of the host. Normally leaf growth slows down in early autumn, ceases in November and does not begin again until March. At the same time the older leaves become hard and brittle so that all the aphids are concentrated on the few remaining healthy ones, leading to a greater percentage of the total population being counted on the single leaf sample. The reverse occurs in March and April when an apparent decrease in population is often recorded, though breeding experiments indicate an increase in the rate of reproduction, due to the plant producing leaves at a relatively higher rate than the population is being built up.

Figs. 5, 7, 9 and 11 show that occasionally the single peak in late May or June was replaced by a more extended period of slightly fluctuating populations, but under these conditions a heavy infestation never developed; average populations rarely exceeded 30 and were more usually under 20 aphids per sample leaf. This was most marked during 1944 in Worcestershire and the Malling district in Kent and, as will be explained later, may be due to climatic conditions. The field of Huxley strawberries sampled in Worcestershire in 1943 (Fig. 9) needs special mention as it is the only occasion in the writer's experience when a high population has been found so early in the season. The curve is not normal as the plants were dusted with nicotine after the first sampling; had this not been done a single peak would probably have occurred in early June and there would have been no secondary peak at the end of the month.

One field in the Isle of Ely (Fig. 11) reached a peak about three weeks in advance of the others in 1943 and again when resampled in 1944. The plants in this field were small with symptoms of incipient chlorosis and probably the lack of vigour

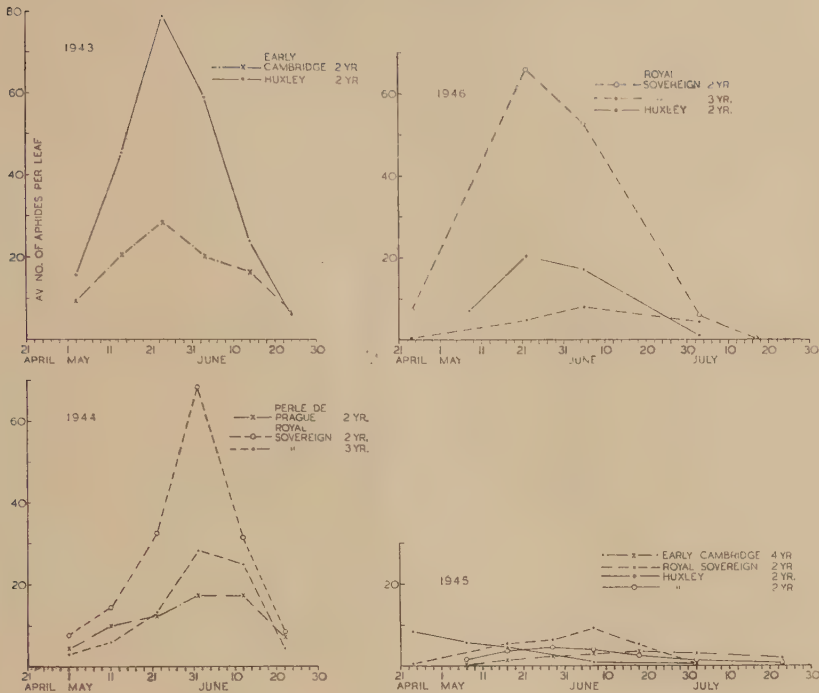


FIG. 5.

Fluctuations in Strawberry Aphid populations on fruiting plants in Hampshire, 1943-46.

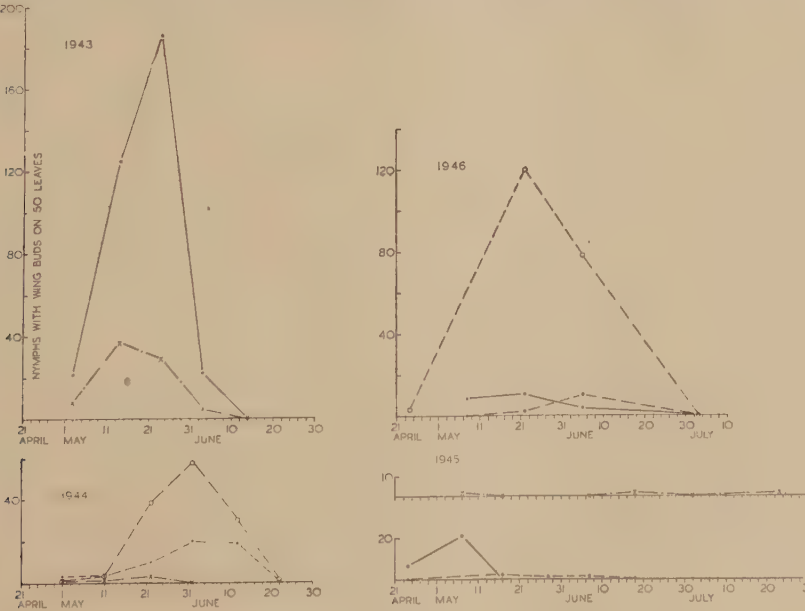


FIG. 6.

Nymphs with wingbuds observed in Hampshire, 1943-46. For corresponding total aphid populations see Fig. 5. The 1945 graphs have been separated for clarity.

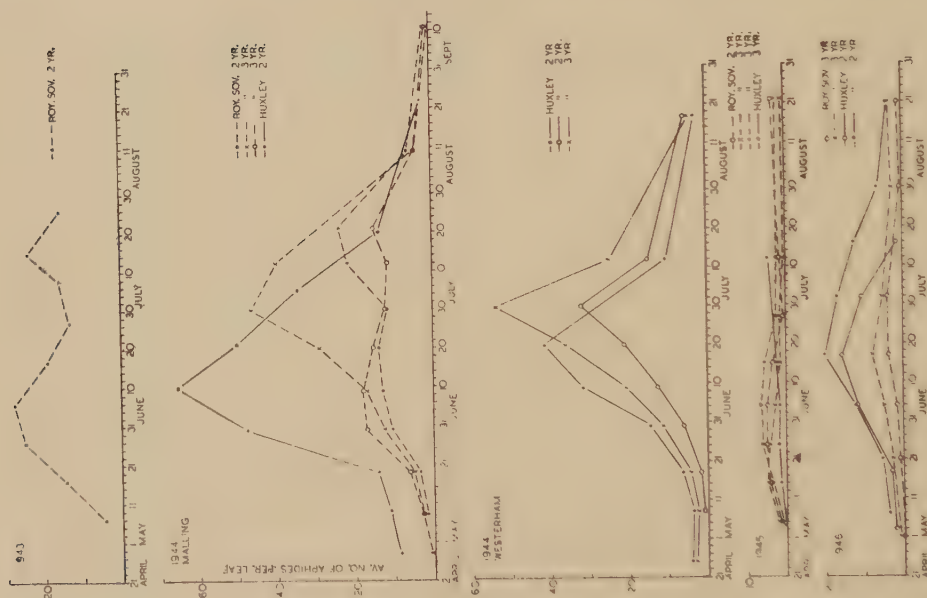


FIG. 7.

Fluctuations in Strawberry Aphid populations on fruiting plants in Kent, 1943-46.

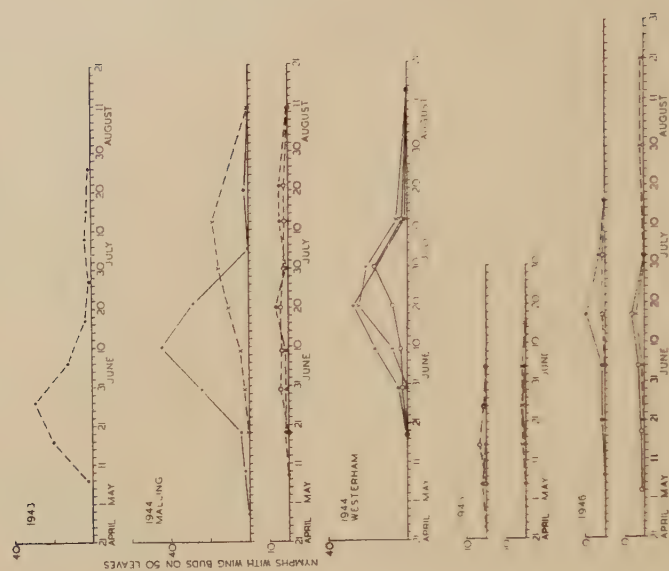


FIG. 8.

Nymphs with wingbuds observed in Kent, 1943-46. For corresponding total aphid populations see Fig. 7.

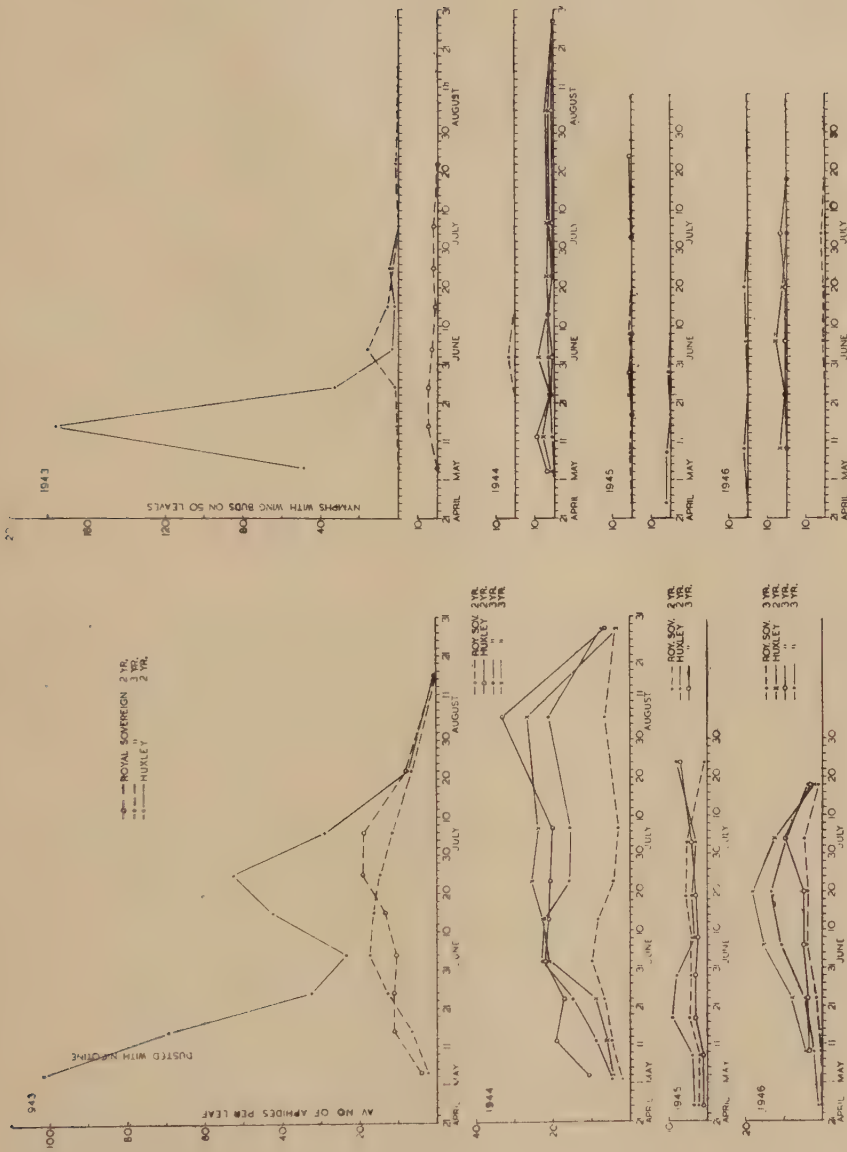


FIG. 9.

Fluctuations in Strawberry Aphid populations on fruiting plants in Worcestershire, 1943-46.

FIG. 10.

Nymphs with wingbuds observed in Worcestershire, 1943-46. For corresponding total aphid populations see Fig. 9.

contributed towards the early peak. Another field in the same area, in 1946, with exceptionally luxuriant foliage, reached a peak after populations in other fields had begun to decline.

Irrespective of the actual intensity of infestation, peak populations occurred at approximately the same date in any one area, the annual variations being less marked than differences due to geographical position. Normally, peak populations occurred earliest in Hampshire, then in Kent and Worcestershire and latest in the Isle of Ely. The Strawberry Aphid was very scarce in Kent in 1943: of about 100 acres inspected only one bed was sufficiently infested to warrant regular counts. Populations remained low throughout the spring of 1945 and the peak period was advanced in all areas except in Hampshire due, in part at least, to the very dry weather which markedly reduced the vegetative vigour of the plants.

Peak populations were normally highest on two-year-old plants, a phenomenon very well illustrated by the fields selected for sampling of which 60 per cent. were of this age. This is mainly due to a high overwintering population caused by the late peak which occurs on first-year plants, leading to two-year-old plants being more heavily infested in the spring when the rapid build-up begins.

The general population trend observed during this investigation is in close agreement with similar studies made in North Wales by Thomas and Jacob (1940), Whitehead and Wood (1946) and Wood (1950).

DISPERSAL PERIODS.

Spring.

The following discussion is confined to observations of winged nymphs on plants over one year of age from the time of planting, i.e. the plants would normally be termed two-year-old or of greater age. Unless heavy aphid infestations are present and no control measures are practised when runners are planted, it is most unusual to find more than an occasional alate aphid developing on strawberries during the spring and summer following planting.

Nymphs with wing buds first appeared soon after the population began to rise in the spring, continued throughout the period of high populations and ceased when numbers became more or less stabilized following the decline. The top graph in Fig. 4 illustrates the normal development when the population rose to a single peak, and Fig. 10 when a fluctuating population occurred over a longer period, as was observed in the Worcestershire fields during 1944. The proportion of the total population which became winged at any time varied from less than one per cent. to slightly over five per cent. and, whilst not statistically significant, there were indications that high populations encouraged the production of alatae. For convenience of illustration the number of winged nymphs on fifty leaves has been plotted, whilst the corresponding graphs representing total aphid populations show the average number of aphids on a single leaf. Where populations were low, it has been necessary, for clarity, to separate some of the graphs. The data have been subjected to various transformations but the resulting graphs, resembling so closely those given by the actual numbers, have not been included.

If the different areas are considered separately, it will be seen that in Hampshire (Fig. 6) small numbers of winged nymphs had begun to appear each year by the beginning of May. Observations did not commence early enough for the first to

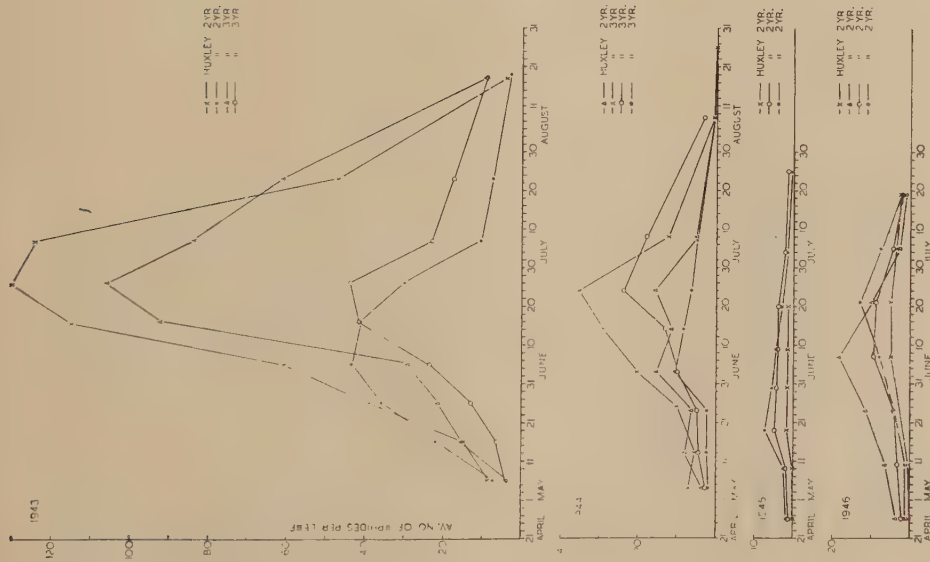


FIG. II.
Fluctuations in Strawberry Aphid populations on fruiting plants in the Isle of Ely, 1943-46.

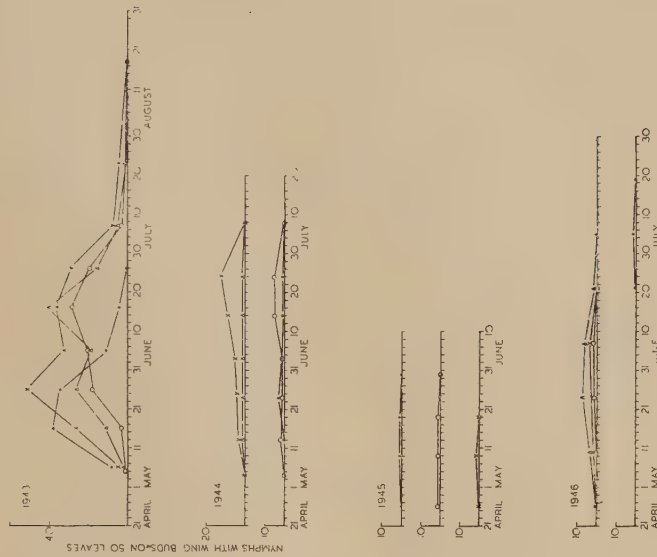


Fig. 12.
Nymphs with wing buds observed in the Isle of Ely, 1943-46. For corresponding total aphid populations see Fig. II.

be recorded with certainty in the majority of fields but it is obvious, by comparing the graphs with those of other areas, that only a few of the earliest were omitted. Peak populations generally occurred during the latter part of May, though in 1945 an exceptionally early peak was noticed on Huxley in early May; this plot was very weedy and the drastic hoeing it received damaged many leaves with the resultant drop in population at a very early date. Very few winged nymphs were found after mid-June and on only one occasion in July.

Fields were sampled annually in the Malling district of Kent and, in 1944, in the Westerham area also. Each year winged nymphs first appeared in the Malling district during early May (Fig. 8), generally rising to a peak about mid-June. It is of interest to note, however, that in the Westerham district, where plant growth is later than around Malling, there was a corresponding delay in the appearance of winged forms. Most winged nymphs had appeared by the end of June, though a few were found in July and, in 1946, a single specimen during August.

The Worcestershire results (Fig. 10) differed from those of other areas in that populations generally remained low and, instead of rising to one well-defined peak, tended to fluctuate over a considerable period. With the exception of the field of Huxley sampled in 1943, few winged nymphs were recorded, but it is clear they began to appear each year at the beginning of May. Due to the longer period before populations declined, winged nymphs also occurred for a greater length of time; most had appeared by the end of June but in many fields some occurred in July and, in 1944, a few in August.

The first winged nymphs also appeared early in May in the Isle of Ely (Fig. 12). The peak period varied considerably in 1943, from mid-May to mid-June; it occurred about mid-June in 1944 and at the beginning of June in 1946; the few winged nymphs recorded in 1945 were all seen during May. This phase was generally over by the end of June though, in 1943 and 1946, a few were observed in July.

Consideration of all the above data shows clearly that winged nymphs began to appear in all areas at approximately the same date. In spite of variations due to seasonal conditions and geographical position this date remained remarkably constant during the years under review, seldom falling more than a week before or after 1st May. With an interval of ten days between successive samplings it was impossible to show fine differences, but there are indications that the first winged nymphs appeared earliest in Hampshire and latest in the Isle of Ely. The full period during which winged nymphs occurred was shortest and most clearly defined in Hampshire where very few were recorded after mid-June; in the other areas small numbers persisted in many fields until the end of June, often into July and occasionally into August.

In Fig. 13 the accumulated total of winged nymphs from all areas at each sampling date is represented graphically as a percentage of the total observed throughout the dispersal period. It will be seen that 95 per cent. had appeared by mid-June in 1943, 1945 and 1946, whilst in 1944, when populations tended to remain at a high level for a considerable time instead of exhibiting a well-defined peak, this figure was not reached until early July. The graphs also show clearly that, although the dispersal period may cover three months, most alatae occurred during a much shorter time. This will obviously have an important bearing on the timing of control measures designed to prevent infestation of first-year beds; it would

seem most desirable to spray during the latter half of May and again immediately the main flight is over, at the end of June.

Autumn.

Following the spring dispersal phase, which ends at the latest in August, there is a period when occasional winged nymphs may be found on first-year plants, but none on older ones. This interval provides an easy means of distinguishing between the spring and autumn phases.

Nymphs with wing buds once more begin to appear in October and may continue until early February, with peak numbers in November or December. The actual period during which winged nymphs are recorded in the samples from any particular field depends largely on the intensity of infestation; where the total number of

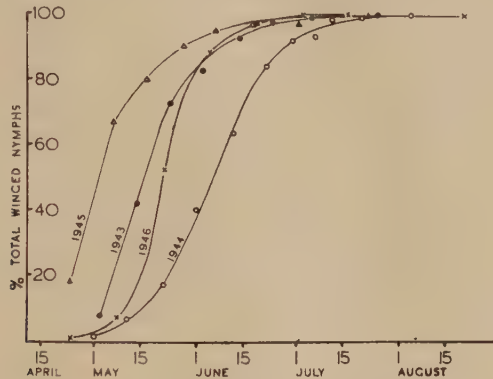


FIG. 13.
Accumulated totals of nymphs with wingbuds from all areas at various dates, expressed as percentages of the total observed during the spring dispersal phase.

aphids is low this form commonly occurs only in small numbers between October and December, whilst in the most densely populated fields such as those illustrated in Fig. 4 it may be present until February. A similar percentage of the total population develops wings as in the spring but as aphids are present in much smaller numbers the winged nymphs are correspondingly fewer. Observations at this time of year have been made only on plots at the Research Station and on commercial farms in Kent but the results probably also apply to other districts.

It has been stated earlier that autumn populations are highest on strawberries planted during the previous autumn or spring, i.e. plants entering their second year, and it is from these that the greatest number of winged nymphs are normally recorded. The middle and bottom left-hand graphs in Fig. 4 illustrate the appearance of winged nymphs on two such plots at the Research Station during 1943-44. The plants were treated with nicotine vapour the previous July, but by October populations had reached a level similar to those on untreated plots and there is no reason to suspect any difference in the behaviour of the aphids. The middle graph is included to show the maximum number of winged nymphs recorded at this time of year in any field during these investigations; generally numbers were much lower, extended over a shorter period and often ceased in December.

On older plants the number of winged nymphs was less and, as shown in the top graph, represented only a fraction of the total appearing during the preceding spring dispersal period. The greatest numbers observed on three-year-old plants of Royal Sovereign and Huxley are shown in the middle and bottom right-hand graphs. It should be pointed out that direct comparisons cannot be made between the graphs for spring and autumn periods because in May and June development of this instar is nearly three times as rapid as in November; also in the autumn, due to the greatly decreased number of living leaves on each plant, a far higher percentage of the population occurs on the sample leaf.

BEHAVIOUR OF WINGED FORMS.

The main function performed by the alate viviparous form of *P. fragaefolii* is to ensure, by dispersal, the survival of the species. All available evidence leads to the conclusion that this aphid has no regular natural host other than the cultivated strawberry. Were it not for infestation of young plants by the winged forms, control would be a very simple matter which, in the course of a few years, might indeed threaten extermination. The preceding section has dealt with the periods when alatae appear, based on records of last instar nymphs with wing buds. As already mentioned, this stage was chosen in preference to the adult to make sure no specimens which had flown in from neighbouring fields were recorded. At the same time any alatae observed on the sample leaves were counted and a comparison of the numbers with those of the winged nymphs has thrown some light on the behaviour of the adult.

TABLE III.

Total numbers of last instar nymphs with wingbuds and alatae in routine population samples.

	May-July (All areas).			October-February (Kent only).		
	Nymphs.	Alatae.	%	Nymphs.	Alatae.	%
1943-4	1,406	66	4.7	366	62	16.9
1944-5	686	51	7.4	98	13	13.3
1945-6	61	4	6.6	68	10	14.7
1946	324	19	5.9	—	—	—

In the left-hand columns of Table III, where these totals are summarized from all fields sampled in Kent, Hampshire, Worcestershire and the Isle of Ely during the spring dispersal phase, it will be seen that each year the number of alatae observed was only about 6 per cent. of the total winged nymphs recorded. A study of the records for individual fields showed the appearance of alatae in the counts to be very sporadic. Where high populations prevailed it was usual to observe most winged forms during the peak periods; at lower levels of infestation there was little correlation between the numbers of alatae and winged nymphs; in many fields alatae were seen on only one or two occasions throughout the dispersal period and

often none was recorded. Breeding experiments did not indicate any mortality during the final moult, so the explanation was obviously associated with the habits of the adult.

Often, in the course of counting, it was noticed that the majority of alatae on the young sample leaves were pale in colour, indicating that they had only recently moulted. Closer inspection of entire plants revealed the presence of mature alatae, i.e. fully chitinized specimens, on the older leaves, often on the upper surfaces; but even when total plant populations were counted the proportion of alatae to winged nymphs was not materially increased. From these observations it is concluded that winged forms departed from the plants on which they were reared shortly after the final moult, otherwise as the season progressed alatae should have accumulated, eventually exceeding the number of winged nymphs present. Furthermore, the marked scarcity of alatae throughout the dispersal phase showed that a considerable proportion did not settle on other plants in the same field but travelled in search of more distant strawberries.

These observations help to explain why Greenslade (1941), who based his results on the presence of alatae, considered the spring dispersal period to be much shorter than that indicated by the current investigation. In fact, had the present writer recorded alatae only, the conclusions regarding the duration of the dispersal period would have been very different from those deduced from records of winged nymphs. The absence of alatae after winged nymphs have been observed on the plants, noted by Greenslade, is a common occurrence in fields where populations are moderate or low and can now be easily explained on the grounds that winged forms depart soon after reaching maturity.

Davies (1935, 1936) has shown that *Myzus persicae* (Sulz.) only flies when temperature, humidity and wind speed are all favourable. The limits set by Davies have been slightly modified by later workers, but it is generally considered that wind speed is the most important factor and voluntary flight is only undertaken when this is less than 5 m.p.h. (Thomas and Vevai, 1940; Broadbent, 1948). Greenslade (1941) found very similar conditions governed the flight of *P. fragaefolii*, but light intensity was also important and, from a study of the meteorological records, showed that conditions conducive to flight seldom occurred for more than a short time each day; often for periods of several days one or more factors were unfavourable, excessive wind speed being the most common. Similar conditions have occurred during this investigation, yet there was no indication that mature alatae were prevented from leaving the plants for any length of time. This leads to the conclusion that the initial flight of winged aphids is primarily governed by the microclimate surrounding the insect and attempts at correlation with data from official meteorological stations may give a serious underestimate of the periods when conditions are suitable for take off from the host. For instance, wind has been considered the major limiting factor, but this is normally recorded at forty feet from the ground, whereas slight irregularities in soil level, weeds or other shelter may well reduce the speed below the critical figure in the immediate neighbourhood of the plant. Broadbent (1948) has shown that the wind speed in and just above a potato crop may be considerably less than that given by standard meteorological records.

In the past there has been little information regarding the behaviour of winged forms during the autumn. Greenslade (1941) obtained evidence of single trap plants being colonized when placed near an infested plot but concluded that there were very

few periods when weather favoured flight. The possibility was not, however, ruled out and instances of virus outbreaks were quoted which, from the time of appearance of symptoms, could be traced to autumn infections. The writer has never yet succeeded in obtaining, by means of trap plants, evidence of dispersal in the autumn, probably due to the relatively small number of alatae produced at this time of year. Positive evidence was, however, obtained in 1950 on larger plots where aphids had been completely eliminated at the end of the spring dispersal phase by spraying with *bis(bis-dimethylamino)-phosphonous anhydride*. Fortnightly counts from the time of spraying, early July, failed to reveal the presence of a single Strawberry Aphid until October, when occasional isolated plants became infested. In two instances an alate viviparous female was observed with a few young nymphs and on other plants small numbers of nymphs were seen; these could only have been deposited by winged aphids.

Autumn and winter population counts, summarized in the right hand columns of Table III, have been made only in Kent. It will be seen that though still low, the proportion of alatae to winged nymphs was higher than during the spring dispersal period. When these data are totalled monthly, as in Table IV, the proportion of alatae is observed to increase as winter approaches, but only in February 1944 was it possible to account for all the winged nymphs by the presence of alatae on the plants. The figures suggest that many alatae do continue to leave the plants during the autumn but not so readily as in the spring. If the disparity between numbers of alatae and winged nymphs is to be explained solely by flight it would seem that the Strawberry Aphid flies in all months from October to January and thus tolerates a much wider range of climatic conditions than at present postulated. Probably mortality is higher among alatae at this time of year, for in autumn the strawberry plant produces leaves with short petioles which lie close to the ground and the aphids, living on the undersides, often get splashed with mud during rain. Whilst apterae are frequently seen encrusted with soil and yet living an apparently normal life the effect may be more serious on alatae, especially if the wings become contaminated with soil or water. Also, from early December onwards an increasing proportion are physically incapable of flight. Firstly specimens are noted with crumpled wings; others, whilst possessing fully chitinated body characters have rudimentary

TABLE IV.

Monthly totals of last instar nymphs with wingbuds and alatae observed in Kent during the autumn and winter.

			1943-4		1944-5		1945-6	
			Nymphs.	Alatae.	Nymphs.	Alatae.	Nymphs.	Alatae.
September	..	..	1	0	0	0	0	0
October	..	..	58	0	36	2	9	0
November	..	..	153	12	41	4	54	9
December	..	..	79	15	19	6	—	—
January	..	..	72	19	2	1	5	1
February	..	..	3	15	0	0	0	0
March	..	..	0	1	0	0	0	0

wings or none at all and, finally, wingless specimens appear with all gradations of chitinization down to forms closely resembling apterae but with slight traces of chitin on the thorax.

At present our knowledge of the behaviour of the autumn alatae is incomplete. There is definite evidence that some disperse in October but neither the proportion nor the period over which flight occurs is known. Compared with the spring forms the autumn alatae are of little importance in spreading virus, because they occur in much smaller numbers and climatic conditions are far less favourable for flight. The observations already mentioned confirming autumn flight were obtained on an established runner bed. There is no evidence that freshly planted runners become infested at this period; when set out, these plants possess only two or three fully developed leaves which soon die off leaving only the crown with partially developed leaves protruding above ground level, thus providing a very small target for the aphid. Further, though many autumn planted beds have been inspected in recent years, no aphids have been found until the spring dispersal period on any in which the runners were dipped before planting.

RATE OF INFESTATION OF CLEAN STRAWBERRIES.

The development of aphid infestation in one-year-old strawberry beds, studied on several occasions, has always followed the same pattern. As an illustration details will be given of observations made on a plot of Royal Sovereign at Harvington, Worcs., in 1943. The runners were fumigated with nicotine before planting and a careful survey at the beginning of May indicated that the plants were still free from aphids. Since the nearest strawberries were 300 yards distant it was felt safe to assume that any infestation developing subsequently would be due to initial colonization by alatae. Between fifty and sixty plants, selected by the method previously described, were inspected at approximately ten-day intervals. At first the population on entire plants was recorded, but after 15th June, due to the increased quantity of foliage, only those aphids on a single, partially open, sample leaf were counted. The increase in aphid population is illustrated in the third column of Table V. Subsequent to 15th June, where no aphids were found on the sample leaf, further leaves were inspected and, if necessary, the whole plant, and according to the presence or absence of aphids the plants were classified as infested or clean. The second column of Table V shows how the percentage infested plants

TABLE V.

Population counts to illustrate the rate of infestation by P. fragaefolii.

Date.	% plants infested.	Mean population per sample plant.	Date.	% plants infested.	Mean population per sample leaf.
5th May ..	0	0.0	25th June ..	69	2.4 *
15th May ..	2	0.04	6th July ..	88	4.6
4th June ..	10	0.2	22nd July ..	100	5.1
15th June ..	55	2.2	16th August	94	7.3

* On this and subsequent dates only one leaf was sampled whereas previous figures refer to total plant populations.

gradually increased until, by the end of July, the sampling suggested that almost every plant had become colonized.

Still more interesting was the distribution of the aphids. Throughout May, apart from an occasional winged form, only nymphs were seen, scattered about on the plants either singly or in small groups of not more than six. Adult apterae first appeared on 14th June, but did not become numerous until ten days later.

During May the slowly increasing population was composed entirely of nymphs deposited by alatae, as shown by the absence of adult apterae in the samples. The first considerable increase in numbers occurred between 4th and 15th June, when adult apterae began to appear, and was mainly due to nymphs produced by the apterous viviparous females, although alatae were also still depositing nymphs. The mean populations in counts subsequent to 15th June are not comparable with the preceding ones as after this date aphids were counted on a single sample leaf; nor do they show the true increase in population, for the plants were producing fresh foliage all the time and, as the aphids became spread over an increasing number of leaves, a smaller proportion of the total was recorded at each sampling date.

The above evidence suggests that alatae do not remain long on any one plant but, having fed and deposited a small number of nymphs, they fly off to another plant and repeat the process. Similar behaviour has been reported by Davies (1934), Doncaster (1943) and Doncaster and Gregory (1948) who studied the movements of aphids within potato crops.

This habit of the alatae may have very serious results if the insect is infected with virus, for it means one aphid may infect several strawberry plants. At the same time, by scattering its progeny over a large area, many plants are colonized at an early stage and, by subsequent plant to plant spread by apterae, a uniform infestation rapidly develops over the entire field. More information is required on the distance alatae will travel. Greenslade (1941) showed that, during the spring dispersal phase, single plants situated beneath trees or in grass up to 400 yards from the nearest source of infestation, became colonized. Field observations suggest much greater distances are covered, as runner beds a mile from the nearest commercial fruiting strawberries are regularly found to be infested, even when the plants have been freed from aphids prior to planting. Some aphids may originate on garden plants situated nearer the runner beds, but the numbers of alatae normally produced on such small plots could hardly account for the general infestations observed in recent years. Aphids possess only weak powers of flight but, once airborne, alatae may drift many miles with air currents.

FACTORS AFFECTING VARIATION IN POPULATION.

The preceding population studies have indicated that two distinct rhythms exist in the annual cycles of the Strawberry Aphid. During the year following planting the population increases gradually, rising to a peak in late summer, then declines as winter approaches. These variations can be attributed to normal seasonal changes in climatic conditions of which temperature is considered the most important component, as illustrated in Fig. 1. In addition there is probably a nutritional effect caused by changes in the host, when length of day may be important, for in spring and summer the strawberry plant is in a state of rapid growth, whilst from November to February it is dormant.

Once the strawberry plant has reached two years of age, a different and more complex rhythm is noticed which is repeated annually until the plant dies. The population rises to a peak in late May or June, then rapidly declines and remains low and relatively constant until a further reduction occurs during the winter months, the latter being comparable to that previously described on one-year-old plants at this time of year. The sudden reversal in population trend noticed every year in May or June cannot be due to climatic factors, as these are then relatively constant, nor can it be due to alatae dispersing for, as mentioned previously, not more than about 6 per cent. of the total population develops wings. Many workers have observed this phenomenon when studying aphids and have considered parasites and predators to be mainly responsible. Thomas and Jacob (1940) concluded that predatory insects and parasitic fungi were the main cause of population decline in the Strawberry Aphid, whilst Wood (1950) observed no predators but laid particular emphasis on the fungus, *Empusa planchoniana* (Cornu) Petch.

During the present investigation no detailed records of aphid enemies were made but, from general observations, evidence has accumulated which suggests that, whilst being contributory causes, parasites and predators were not primarily responsible for the sudden decline in population :

(1) The Strawberry Aphid is virtually free from attacks by parasitic insects. Since 1943 not more than a dozen parasitized aphids have been observed ; from these, *Aphelinus asychis* Walker and an undetermined species of *Aphidius* have been bred.

(2) Parasitic fungal attacks occurred very sporadically ; in many fields no sign of any entomophagous fungus was seen during the population studies.

(3) Except in the Wisbech area during 1943, predatory insects never occurred very commonly. Those most generally observed were larvae of *Tachyporus obtusus* L. and *T. hypnorum* F. (Col., Staphylinidae) (Dicker, 1944) and *Anthocoris nemorum* L. (Hem.-Het., Anthocoridae), but no obvious relation was noticed between numbers of aphids and of predators. Some fields appeared to be almost free from predatory insects.

(4) Irrespective of the absence or abundance of parasitic fungi and predators, of the actual number of aphids present and of the age of the plants, providing they were not less than two years old, peak populations occurred in all fields in any one area at the same time ; reasons have already been suggested to account for the most obvious exceptions. It is highly unlikely that predatory and parasitic attacks would occur with such regularity as to cause simultaneous reductions in populations as indicated in Figs. 5, 7, 9 and 11.

(5) Peak populations occurred much later on one-year-old plants, though on these there may have been insufficient time for an effective resident population of predators to become established. However, annual crops infested with aphids often attract large numbers of predators and a similar effect should occasionally be noticed on strawberries during the first year, especially those planted adjacent to older beds.

If parasites and predators are not primarily responsible then what are the main factors influencing population changes? This question is still largely unanswered, although it will be shown that the host plant itself probably plays a major part. But first it is necessary to describe briefly the growth phases of the

strawberry. In the first year, growth continues at a fairly uniform rate throughout the spring and summer and normally the plants carry only a very light crop of fruit. Older plants pass through a phase of vegetative growth in the spring which reaches a maximum in late April or early May; then, as the blossom trusses appear, the number of new leaves decreases and they become still fewer as the fruits develop and ripen. Fruits begin to ripen at the end of May in Hampshire, during the first half of June in Kent and Worcestershire and a little later in the Isle of Ely. Following the fruiting period, more leaves are again produced.

Comparing the population curves with plant development, it will be seen that the period of rapid increase occurred towards the end of the flush of spring growth and, in general, peak populations coincided with the ripening of the earlier fruits. It would seem, therefore, that if the host is primarily responsible, factors associated with fruit development may be intimately connected with the decline in population. Strong support for this theory was obtained in 1944 when serious frosts, on the nights of 7th-9th May, destroyed a large proportion of the strawberry crop in Kent and Worcestershire. At the time, four fields were under observation in the Malling district of Kent, three of Royal Sovereign which were estimated to have lost 80 per cent. of the normal crop, and one of Huxley where frost damage was almost negligible. The three fields of Huxley and one of Royal Sovereign sampled in Worcestershire all suffered a great reduction in crop. Figs. 7 and 9 show that in all the fields subject to severe frost injury the aphid populations did not follow the normal pattern. Instead, after the initial increase in May, a peak was reached in early June, populations then remained fairly constant until late July or early August when, following a second peak, they declined to the normal summer level. One of the Kent fields was exceptional in that the population after a slow initial increase rose to a single peak in early July; this may have been due to the plants in this field being far more vigorous than in the others. By contrast the population curve for the Huxley field where frost injury was negligible followed the normal pattern, as did the curves for three more fields of Huxley at Westerham where again no loss of crop was caused by frost.

An experiment to study the effect produced by frost on leaf development was carried out on two-year-old Royal Sovereigns in 1947. Frost injury was simulated by removing all the blossoms, producing a slightly more drastic effect than occurred in 1944, as in that year a few late berries matured. The results, illustrated in Fig. 14 were obtained from twelve plots each of nine plants, half of which were deblossomed on 5th May when the first blossoms opened and subsequently as necessary, and the others allowed to carry a normal crop. At each inspection the petioles of new leaves were marked with indian ink. On fruiting plants, leaf development continued to decrease from the time of blossoming until all the fruit had ripened, whilst, where blossoms were removed, this effect was reduced and the number of leaves began to increase at an earlier date. Approximately 60 per cent. more leaves were produced during May and June on the deblossomed plants but most marked of all was the quality of the foliage. On fruiting plants the leaves were small with short petioles, of a dull colour and harder texture; those on the deblossomed plants were similar in size and colour to the leaves produced prior to the blossom period. In addition to the actual leaf counts one general observation may be of importance. The period of ripening coincided with a dry spell and it was observed that plants carrying the normal crop wilted during the hottest part

of the day, whilst the deblossomed ones, though possessing a much larger leaf area, showed no such effect.

Combining the experimental and field observations, the atypical population curves obtained in 1944 may be explained on the grounds that destruction of blossoms by frost stimulated the plants to greater leaf development, which provided enough food to sustain a higher aphid population for a longer period than was possible on fully fruiting plants. Probably of greater importance than the actual number of leaves is the nourishment afforded by the leaf to the aphid, a factor which has not been assessed, though from visual inspection the leaves of deblossomed

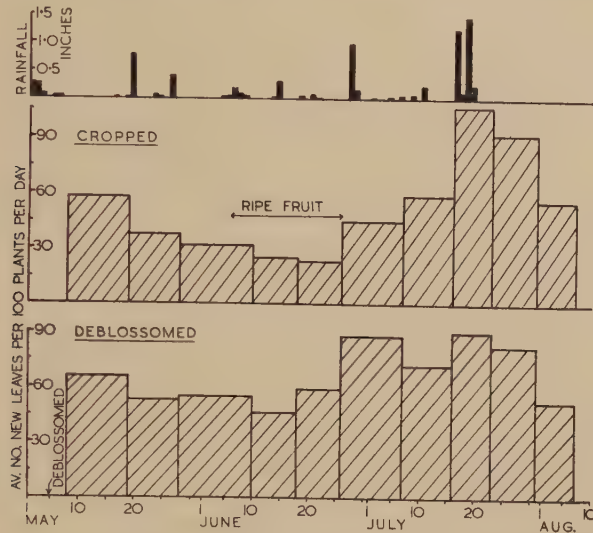


FIG. 14.

Numbers of leaves produced by fruited and deblossomed two-year-old Royal Sovereign plants, 1947.

plants appeared to be far superior in this respect. There is thus some evidence that nutrition is the primary influence in controlling aphid populations on strawberries during the early summer months and the correlation previously noticed between peak populations and ripening of the fruit was in reality due to suppression of leaf development whilst fruits were maturing and ripening.

There is further evidence to support this hypothesis :

(1) On first-year plants, which continue growth at a fairly uniform rate throughout the summer and where the quantity of fruit produced is normally insufficient to affect leaf development, the population rises to a peak at a later date than on older fruiting plants.

(2) One field of strawberries sampled in the Isle of Ely both in 1943 and 1944 developed a peak in advance of the other fields. As already mentioned, the vigour of these plants was low and field notes made at the time indicated a premature reduction in the number of young leaves. In contrast, an exceptionally vigorous

stock sampled in the same area in 1946 reached a peak at a later date than other fields.

Recent investigations by Kennedy, Ibbotson and Booth (1950) have shown that *Myzus persicae* (Sulz.) and *Aphis fabae* Scop., when bred on spindle trees or sugar-beet, both show marked preferences for developing and senescing leaves as compared with mature leaves. Ibbotson and Kennedy (1950) have further demonstrated that with *A. fabae* the most restless forms are the adult apterae and older winged nymphs. Whilst no detailed records are available for the Strawberry Aphid, numerous observations indicate that this species similarly prefers young leaves, though there is no information available with regard to senescing leaves; also the young leaves are usually first colonized by adult apterae.

With these additional facts it is possible to elaborate the hypothesis to account for the summer decline in population. As fruit development proceeds leaf development decreases; not only is there a progressive reduction in the size and number of young leaves but a nutritional factor probably also comes into play making them less attractive than previously. As aphids, especially adult apterae, leave maturing leaves and find no suitable young leaf present on the plant, a general dispersal occurs but, all plants being in the same unattractive condition, an increasing proportion of the population becomes restless and the reproductive rate drops. This movement of adult apterae would provide an explanation for the impression so frequently obtained during field counts at fruiting time that the population on sampled leaves consisted mainly of nymphs. Doubtless there are other factors also, such as physiological changes in the plant associated with fruiting, about which little is known to plant physiologists and nothing of their effect on the insect.

The foregoing is not claimed to be a complete explanation. For example, unless there is a critical period when these factors become operative, a more gradual change in population would be expected than is indicated in the population curves of heavily infested strawberries. Neither will this hypothesis explain why the population remains so low following the fruiting period when it is known that there is an increase in the rate of leaf production.

SUMMARY.

The synonymy and host plants of the Strawberry Aphid, *Pentatrachopus fragaefolii* (Cock.) are discussed; the rate of development of the nymph and fecundity of the apterous adult have been studied under insectary conditions.

Intensive sampling of selected infested fields throughout the year in Kent and from May to July in Hampshire, Worcestershire and the Isle of Ely during the period 1943-46 have shown that two distinct rhythms exist in the annual cycles of this aphid. On first-year plants the population rises to a peak in late summer or early autumn, then declines, whilst on older plants a peak is reached in late May or June followed by a rapid decline with low populations persisting for the rest of the year. Alatae occur from early May until late June or July and in greatly reduced numbers from October until January or February. The behaviour of the winged forms is discussed and the mode of infestation of clean strawberry beds is described.

Evidence is presented to suggest that the rapid decline in populations during June on plants over one year old is primarily due to a reduction in the number and quality of the young leaves produced at that time as a result of fruit development.

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The author gratefully acknowledges the help given by Dr. S. C. Pearce for advice on sampling techniques, by Mr. J. B. Briggs who was responsible for insectary records during experiments on nymphal and adult development, by the horticultural officers in locating suitable fields for sampling and by the growers who permitted frequent inspections.

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METABOLISM OF SUCROSE IN APPLES I.

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INTRODUCTION.

IN two previous papers (6 and 7) we have discussed respectively the starch metabolism and the acid metabolism of the apple, on the basis of experimental results obtained during a number of years. These papers, together with a full description of the methods of sampling and analysis (2) have already been published in this journal. In the present communication the metabolism of cane sugar in the apple is considered on the basis of the same data.

It may be recalled that the analyses were of samples of fruit, taken from the tree and subsequently from storage at various constant temperatures. The experiments cover a number of seasons and a number of gatherings at various stages of growth. The growth period studied is that between early June and October, which is the period of growth by cell-enlargement. In relation to the following study of the metabolism of sucrose, we recall that at the beginning of this period no starch is present in the fruit and that the starch content reaches its maximum (approximately 2 per cent.) about the middle of August in the case of Bramley's Seedling apples, and about a week or so earlier in the case of Worcester Pearmain apples, and then gradually falls to a zero value later in the season. The storage of the gathered fruit at constant temperatures was continued up to the point when rotting or functional breakdown began to appear in the stored samples.

For reference, the populations of Bramley's Seedling and Worcester Pearmain apples dealt with here are shown in Table I. In the text and figures the experiment numbers used in the publication of the original data are shown in brackets.

BRAMLEY'S SEEDLING POPULATIONS COMPARED IN A PRELIMINARY MANNER.

Figure 1 shows the changes in sucrose concentration (grams per hundred grams fresh weight) during the main period of growth. Figure 2 shows the changes in the concentration of starch (grams per hundred grams fresh weight) also during the main period of growth. In these figures the dotted line represents the results obtained during growth by Archbold (1).

In Experiment 1 (IV) both starch and sucrose content are high: in Experiment 6 (VII) starch is high, but sucrose is normal or below normal and the glucose content is unusually low. In Experiment 7 (I) starch is normal, but sucrose is high. A high content of sucrose in this case, and also in the case of Experiment 1 (IV), is associated with a high fructose content.

In Figure 3 fresh weights are plotted against time. It will be seen that 1 (IV), 6 (VII) and 7 (I) are populations in which the size of the fruit increased more rapidly than in the other cases.

TABLE I.

Reference number in this paper.	Experiment number (original data (2)).	Date of gathering.	Average fresh weight (g. per apple).	Initial Values (g. per 100 g. fresh weight)				Storage temperature (°C.).	Orchard.*
				Sucrose.	Starch.	Glucose.	Fructose.		
<i>Bramley's Seedling Apples.</i>									
1.	IV	23.6.33	30.00	0.77	0.89 [†]	0.64	1.78	3° and 10°	A
2†	V	10.7.34	30.00	0.58	0.88 [†]	1.05	1.68	1°, 3°, 10°, 15° and 20°	A
3	VIII B	24.7.39	52.00	0.94	1.14	0.87	1.98	10°	A
4	VIII C	14.8.39	72.08	1.30	1.39	—	—	10°	A
5	II A	31.8.31	112.60§	1.68	1.32 [†]	1.18	3.26	10°	B
6	VII	24.9.37	135.70	1.87	2.03	0.63	4.13	1°, 5°, 10°, and 15°	A
7	I	28.9.28	168.50	3.58	0.62 [†]	1.13	5.63	1°, 3°, 5°, 10°, 15° and 22.5°	C
8	II B	1.10.31	106.20§	2.60	0.44 [†]	1.34	4.31	10°	B
9	VIII D	2.10.39	108.60	2.43	0.62	—	—	10°	A
<i>Archbold (1932)</i>									
"		17.6.30	5.77	0.31	0.12	0.69	0.58		D
"		24.6.30	13.31	0.47	0.12	0.82	0.77		D
"		3.7.30	24.88	0.42	0.38	0.94	1.24		D
"		14.7.30	37.64	0.70	0.84	1.12	1.55		D
"		28.7.30	54.35	1.37	1.03	1.20	2.16		D
"		11.8.30	78.50	1.54	1.26	1.20	2.77		D
"		26.8.30	87.94	1.93	1.46	1.16	3.32		D
"		8.9.30	101.89	2.09	0.91	1.22	3.74		D
"		22.9.30	123.10	2.54	0.70	1.17	3.90		D
"		7.10.30	138.17	2.93	0.14	1.52	4.10		D
"		21.10.30	150.68	2.91	nil	1.34	4.37		D
<i>Worcester Pearmain Apples.</i>									
	VI A	18.7.35	25.6	0.51	1.92	1.47	3.29	10°	E
	VI B	29.7.35	37.2	0.71	2.09	1.44	4.34	10°	E
	VI C	15.8.35	62.8	1.48	2.17	1.18	5.76	10°	E
	VI D	2.9.35	69.8	1.98	1.52	1.18	6.43	10°	E
	III	3.9.31	70.0	1.88	0.55 [†]	1.55	5.90	1° and 10°	E
<i>Archbold (1932)</i>									
"		27.5.30	0.048	0.48	nil	0.86	0.32		D
"		30.5.30	0.10	0.11	nil	0.65	0.48		D
"		2.6.30	0.21	0.15	nil	0.62	0.46		D
"		5.6.30	0.50	0.18	nil	0.67	0.56		D
"		11.6.30	1.78	0.22	nil	0.83	0.50		D
"		17.6.30	4.28	0.20	nil	1.03	0.75		D
"		24.6.30	6.20	0.64	0.21	1.50	0.96		D
"		3.7.30	11.22	0.44	0.89	1.84	2.20		D
"		14.7.30	21.77	0.78	1.68	1.80	3.23		D
"		28.7.30	38.00	1.30	2.01	1.43	4.40		D
"		11.8.30	56.57	1.97	1.96	1.20	5.46		D
"		26.8.30	72.64	2.85	1.29	1.27	6.39		D

* Orchards:

- A. Farningham, Kent.
- B. Shippea Hill, Cambridge.
- C. East Malling, Kent.
- D. Swanley, Kent.
- E. Cottenham, Cambridge.

[†] Also stored at 10° C. in N₂ (less than 0.5% oxygen), O₂ and gas mixture (20% O₂, 10% CO₂, 70% N₂).

[‡] These values are probably 0.1-0.2 high as compared with the others in the column because the estimations were made without extraction of the alcohol-insoluble residue with potassium oxalate, and correspond to fractions A+B+C whilst the others correspond to fractions A+C as defined in a previous paper (6).

[§] It should be noted that in the case of Experiments 5 (II A) and 8 (II B) the samples at the two gatherings could not have been representative of the population with regard to size, since the average weight of the apples gathered at the later date was actually smaller. This fact has nevertheless little apparent effect on the relative positions of the amount of starch and of sucrose per apple or on the amount of sucrose per hundred grams fresh weight.

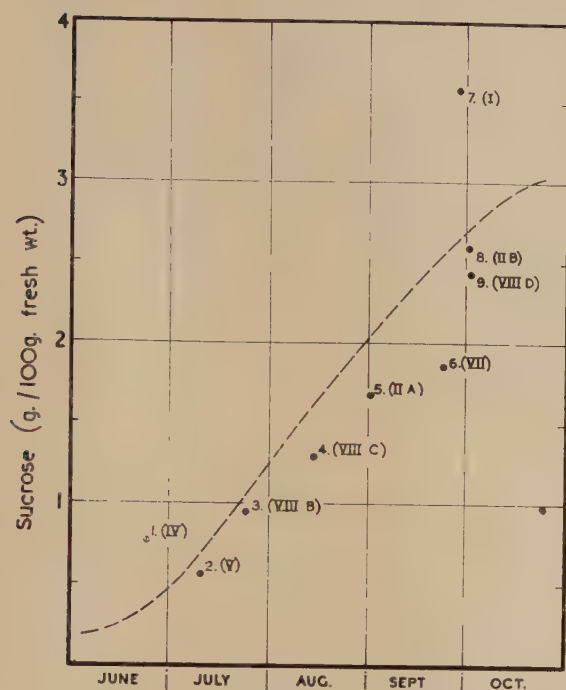


FIG. 1.

Percentage of sucrose in Bramley's Seedling apples at the time of gathering.

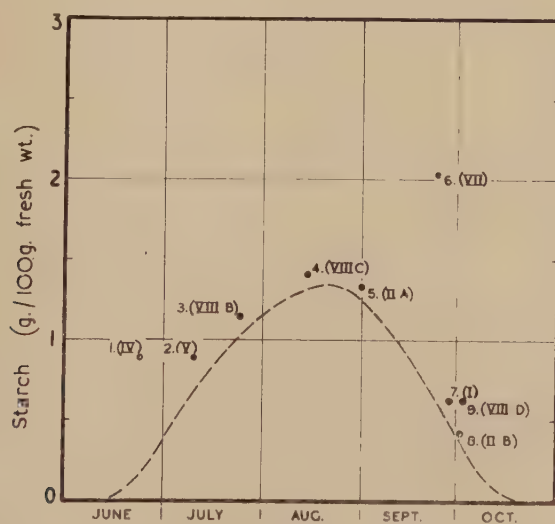


FIG. 2.

Percentage of starch in Bramley's Seedling apples at the time of gathering.

PROGRESS CURVES OF SUCROSE CONTENT (BRAMLEY'S SEEDLING APPLES) EXPRESSED AS GRAMS PER APPLE. THE CLIMACTERIC RISE IN RESPIRATORY ACTIVITY.

Figures 4 and 5 show both the progress of the accumulation of sucrose per apple during growth (Archbold (1)) and the change in sucrose per apple after gathering while in storage at 10° C. (our experiments). Except in the case of the

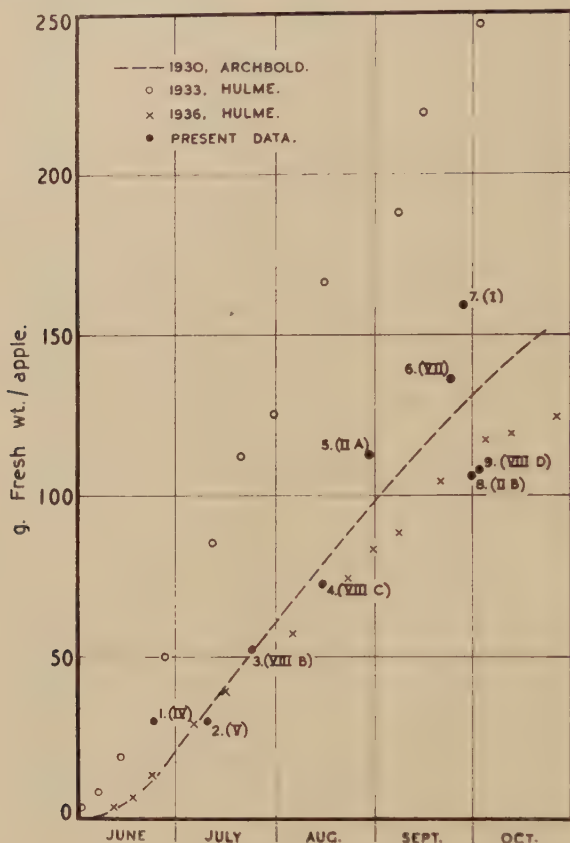


FIG. 3.
Fresh weight per apple (Bramley's Seedling) at the time
of gathering.

two latest gatherings, sucrose continues to accumulate in the fruit after gathering at a rate which initially may be equal to the rate of accumulation on the tree. A maximum content is reached, and subsequently the sucrose in the system steadily diminishes. Inspection shows that the rise in sucrose content after gathering occurs during the period of starch degradation. The process of loss of sucrose is prolonged, and the curves showing the amount present plotted against time are broadly similar in all cases, being of a type which suggests that the rate of loss may be a function of the amount present. The formal method adopted in smoothing the curves is explained in the following section.

It can also be seen from Figures 4 and 5 that the decline in sucrose content is not proceeding to a zero value. In the earlier gatherings the sucrose content, after reaching an approximately steady state at a low value, again rises during the period of the climacteric rise in respiratory activity, after which it falls, but not towards a zero value. In the later gathered populations the climacteric intervenes while the sucrose content is still rapidly falling. The occurrence of the climacteric in these cases does not appear to have a noticeable effect on the form of the downward drift of sucrose content. In the case of Experiment 4 (VIII C) and of Experiment 5 (II A) it can clearly be seen that the downward drift is not towards a zero value.

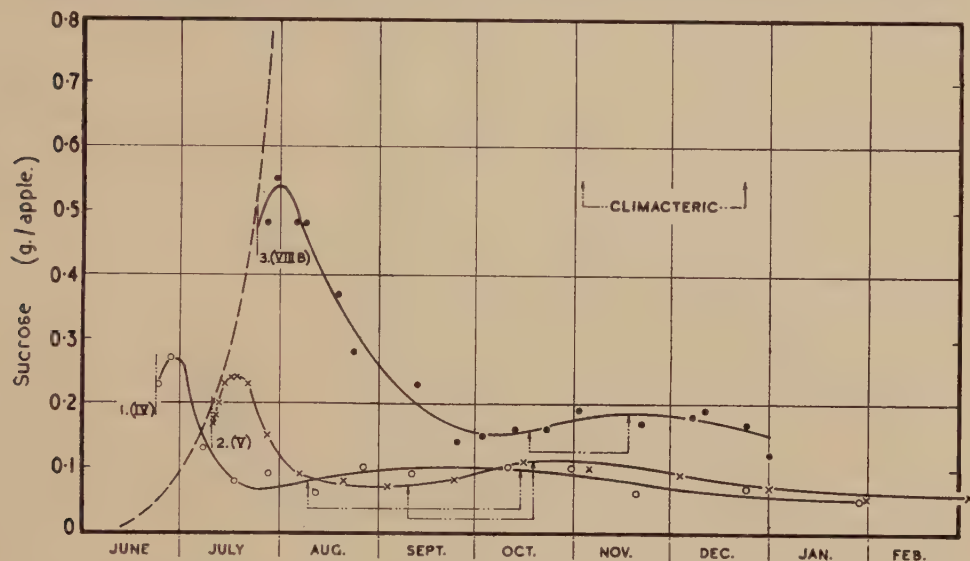


FIG. 4.

The accumulation of sucrose in Bramley's Seedling apples during growth (interrupted line), and the change in sucrose during storage at 10° C. after gathering (continuous lines).

It is presumed that the same is true of the later gatherings. In these cases, owing to the greater amount of sucrose present at gathering and to the shorter storage life of the fruit, the storage life ends before the sucrose content has reached a steady state.

FORMAL ANALYSIS OF THE CURVES OF SUCROSE LOSS IN BRAMLEY'S SEEDLING APPLES DURING STORAGE AT 10° C. THE RATE CONSTANT OF SUCROSE LOSS.

We have found that, subsequent to the point in time at which starch has disappeared, the observations of sucrose content fit a curve with the following formula :

$$\log (c-m)=b-at$$

in which c is the observed sucrose content (grams per hundred grams original fresh weight) ; m the "steady state" value ; b the initial value* ; a the rate constant ; and t the time in days.

The results are presented in Table II and Figures 6 and 7. The initial rise and fall in the sucrose content during the course of starch degradation is shown in these

* The initial value is found during the procedure in which the straight line of best fit is drawn by the method of least squares to plottings of $\log (c-m)$ against time.

figures by a dotted line drawn by eye judgment through the observed points. The values of m , which we have used, have been judged in the case of the four earliest gatherings, by inspection of progress curves of sucrose content against time. In the case of the later gatherings the values of m are only presumed. Where the presumed value of m is large in relation to the value of c , as in the case of the two earliest gatherings (Experiments 1 (IV) and 2 (V)), a relatively small change in the

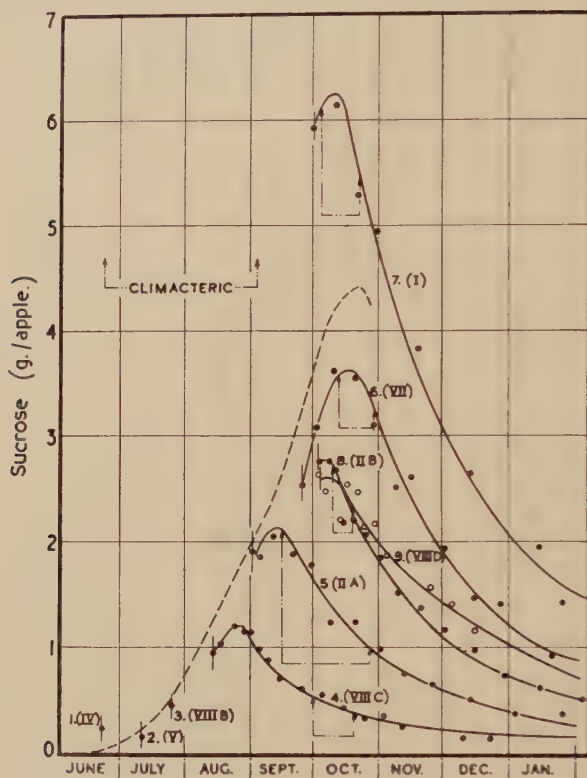


FIG. 5.

The accumulation of sucrose in Bramley's Seedling apples during growth (interrupted line), and the change in sucrose during storage at 10° C. after gathering (continuous lines). In Experiment VIII D the apples were post-climacteric when gathered.

value of m makes a considerable difference to the value of the rate constant. For these cases two values corresponding to two possible m values have, therefore, been given in Table II in order to demonstrate the extent of the tolerance to be allowed. The standard deviation of the scatter of the observations about the calculated curve has been determined in each case and compared with the standard deviation of the replicate initial samples about their mean in each case. The former range from ± 0.03 to ± 0.13 and the latter range from ± 0.03 to ± 0.15 .

Figure 7 shows the above procedure applied to the results obtained from Experiments 2 (V), 6 (VII) and 7 (I) at storage temperatures ranging from 1° C. to

TABLE II.

Values for the rate constants ($a \times 10^2$) of sucrose loss in apples stored in air except where otherwise stated.

Reference No. in this paper.	Experi- ment No. (original data (2)).	Date of gather- ing.	Temperature (°C.).							Respiratory activity (c.c. CO ₂ per 10 K.H. at 10° C. at time of gathering).	Protein nitrogen (% fresh weight) for a single population of 1936 (5) on dates corresponding to those of Column 3.
			1°	3°	5°	10°	15°	20°	22.5°		
<i>Bramley's Seedling Apples.</i>											
—	VIII A†	19.6.39	—	—	—	—	—	—	—	216	0.100
I	IV	23.6.33	—	2.267 (-0.30)	—	6.860 (-0.20) or 4.173 (-0.10)	—	—	—	134	0.076
2	V	10.7.34	1.374 (-0.40)	1.587 (-0.34)	—	4.378 (-0.20) or 6.56 (-0.25) 4.228* (-0.30)	7.945 (-0.15)	8.438 (-0.10)	—	81	0.045
3	VIII B	24.7.39	—	—	—	1.957 (-0.31)	—	—	—	79	0.032
4	VIII C	14.8.39	—	—	—	1.332 (-0.30)	—	—	—	66	0.031
5	II A	31.8.31	—	—	—	1.094 (-0.30)	—	—	—	62	0.028
6	VII	24.9.37	0.331 (-0.45)	—	0.553 (-0.37)	0.844 (-0.30) 0.835† (-0.30)	1.691 (-0.25)	—	—	57	0.026
7	I	28.9.28	0.240 (-0.45)	0.303 (-0.39)	0.365 (-0.37)	0.695 (-0.30) 0.906 (-0.30)	1.094 (-0.25)	—	2.337 (-0.21)	47	0.026
8	II B	1.10.31	—	—	—	0.906 (-0.30) 0.619 (-0.30)	—	—	—	48	0.026
9	VIII D‡	2.10.39	—	—	—	0.619 (-0.30)	—	—	—	—	0.026
<i>Worcester Pearmain Apples.</i>											
—	VI A	18.7.35	—	—	—	2.150 (-0.25)	—	—	—	—	—
—	VI B	29.7.35	—	—	—	1.729 (-0.30)	—	—	—	—	—
—	VI C	15.8.35	—	—	—	1.798 (-0.42)	—	—	—	—	—
—	VI D	2.9.35	—	—	—	1.676 (-0.50)	—	—	—	—	—
—	III	3.9.31	0.764 (-0.20)	—	—	1.970 (-0.25)	—	—	—	—	—

The figures in brackets are the values we have used for the constant m.

* Stored in 100% oxygen.

† Stored in air containing one part in five hundred of ethylene. In air the climacteric rise in respiratory activity occurred between the 16th and the 42nd day (44 to 63 c.c. CO₂ per 10 K.H.). In the presence of ethylene the maximum value of 65 c.c. CO₂ per 10 K.H. was attained within two days of gathering and then remained steady.

‡ No record of respiration was obtained for Experiment 9 (VIII D). There was, however, in this experiment an earlier gathering (VIII A), on 19th June, for which a record of respiratory activity at 10° C. was obtained, but on which no chemical analyses were carried out.

22.5° C. A new point emerges here, namely, that the "steady state" value of sucrose content is higher the lower the temperature. This point seems so important that the critical evidence, i.e. the progress curves of sucrose content for Experiment 2 (V), is given in Figure 8. The degree of the coincidence of the climacteric rise in respiratory activity with the rise in sucrose content can be judged from this figure.

STAGE OF GROWTH AND THE RATE CONSTANT OF SUCROSE LOSS.

The progress of sucrose loss is assumed for the present to be a process of hydrolysis, partly an acid hydrolysis in the vacuole, but mainly an enzyme-catalysed hydrolysis taking place in the cytoplasm. Thus, as previously reported by Hanes and Kidd (3), "in Bramley's Seedling apples containing initially 3.5 per cent. of

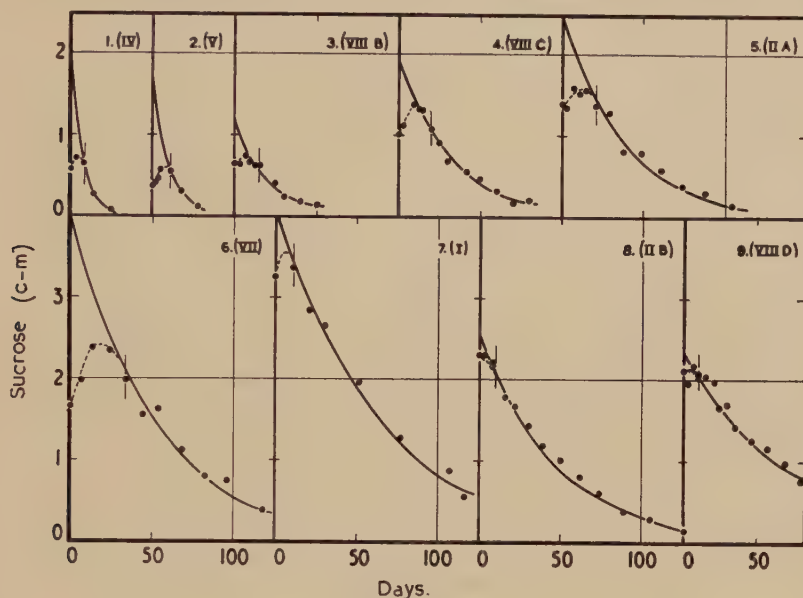


FIG. 6.

Logarithmic fall in sucrose content of Bramley's Seedling apples during storage at 10° C. (see text). The vertical lines indicate the time at which starch has disappeared from the system.

sucrose, the initial rates of "hydrolysis" at 22.5°, 15° and 10° C. were found to be 4.3, 1.9 and 1.0 per cent. of the total sucrose per day; the predicted acid-hydrolysis values (pH 2.9) for these respective temperatures are 1.1, 0.39 and 0.19 per cent., values which represent only about one-quarter to one-fifth of the observed rates *in vivo*".

Figure 9 shows the rate constants of sucrose loss and the values for respiratory activity at 10° C. plotted against the date of gathering. The activity of sucrose loss appears to fall during growth in a manner generally similar to the fall in respiratory activity, in other words, rapidly at first and then more slowly.

Respiratory activity in apples has been found by Hulme (4) to be closely correlated with protein content. More critically considered, the age/sucrose loss-activity curve, even allowing for the large degree of uncertainty attaching

to the points for Experiments 1 (IV) and 2 (V), has a greater fall than the curves for respiratory activity and for protein content. It should, therefore, be borne in mind that loss of sucrose may be a function not only of protein content, but also of a diffusion factor. The area of the vacuole/cytoplasm interface offers a possible explanation of such a diffusion factor. This area (in $\text{mm}^2 \times 10^{-4}$ per gram fresh

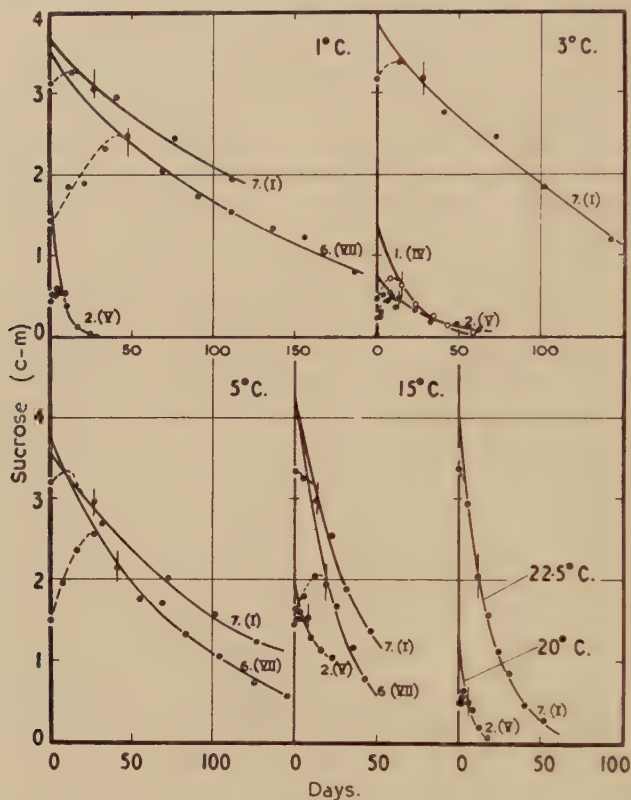


FIG. 7.

Logarithmic fall in sucrose content of Bramley's Seedling apples during storage at various temperatures (see text). The vertical lines indicate the time at which starch has disappeared from the system.

weight) falls between 11th June and 6th July from 9 to 4.5, and thereafter, to 1st October, to 3.*

TEMPERATURE AND THE RATE CONSTANT OF SUCROSE LOSS (BRAMLEY'S SEEDLING APPLES).

The results obtained at different temperatures of storage in the case of Experiments 2 (V), 6 (VII) and 7 (I) are brought together in Table III and Figure 10. The results for the three different populations agree satisfactorily, with the exception of the value at 20°C. for Experiment 2 (V). This is low and

* See previous publication (7), Table V.

suggests the possibility of a maximum activity at about 18° C. in this case. In Table III the corresponding results obtained for the activity constants of starch degradation (6) and of acid loss (7) are also given.

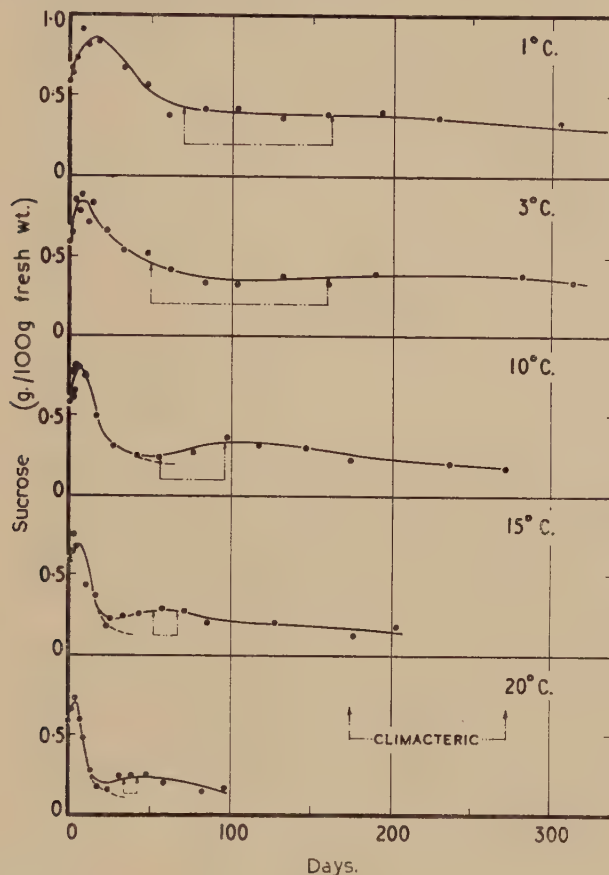


FIG. 8.

Course of change in sucrose content of Bramley's Seedling apples at different temperatures (see text).

The temperature coefficient of sucrose loss is markedly greater than that of starch degradation. Assuming sucrose loss to be going on all the time and assuming a direct connection between starch degradation and sucrose formation—a subject to

TABLE III.

Temperature.	1° C.	3° C.	10° C.	15° C.	20° C.
Relative rate of :					
Sucrose loss	1	1.2	2.9	4.7	7.8
Starch degradation	1	1.2	1.8	2.36	2.74
Acid loss	1	1.15	1.9	3.0	6.1

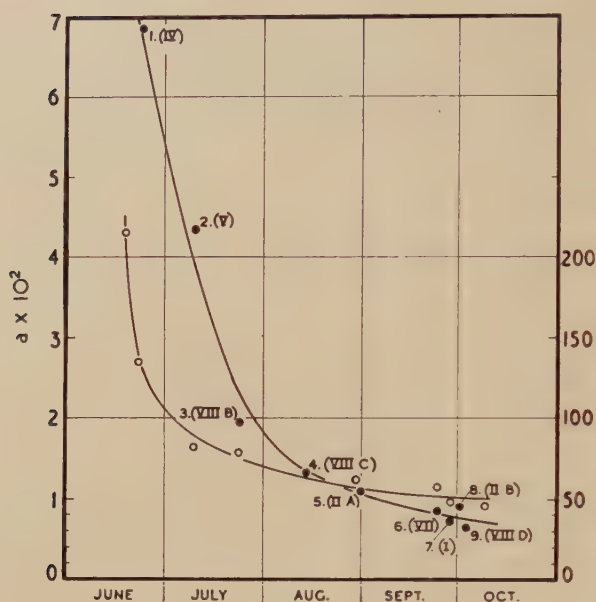


FIG. 9.

Rate constants ($a \times 10^2$) of sucrose loss for Bramley's Seedling apples at different stages of maturity (dots) compared with the rate of CO_2 -production, at 10°C . (circles).

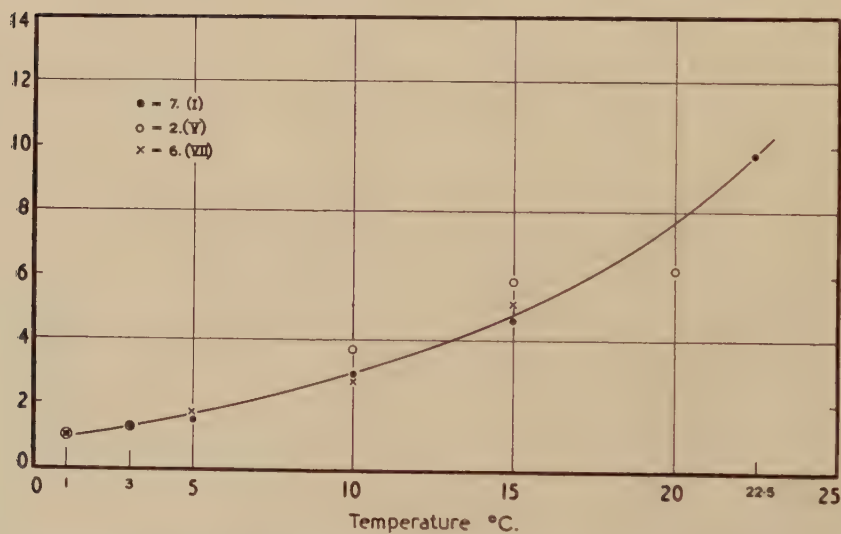


FIG. 10.

Rate constants ($a \times 10^2$) of sucrose loss for Bramley's Seedling apples at different temperatures relative to unity at 1°C .

be fully discussed in Part II of this paper—it is to be expected that the rise in sucrose content which takes place during starch degradation after gathering, will be less at high temperatures than at low temperatures. Reference to Figures 7 and 8 shows that this is, in fact, so.

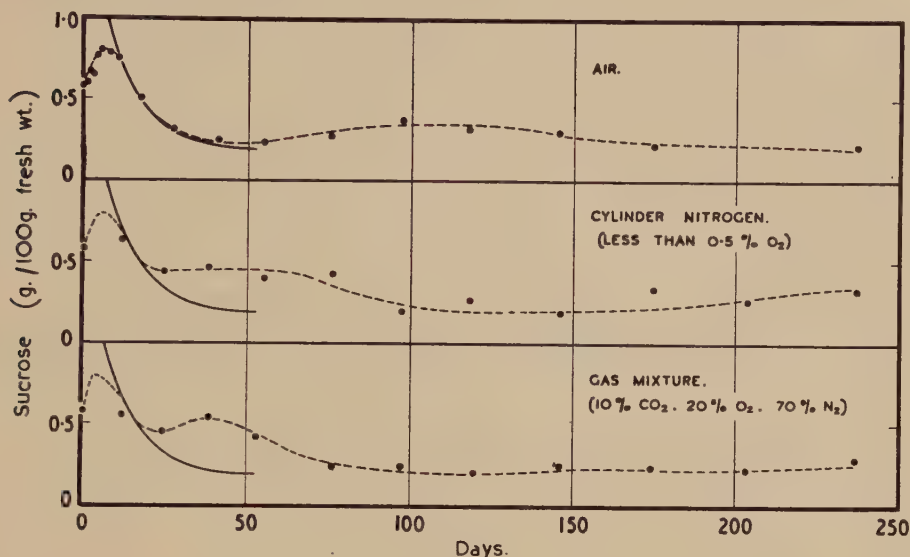


FIG. 11.

Course of change in sucrose content of Bramley's Seedling apples in an atmosphere of very low oxygen content and in an atmosphere containing 10 per cent. carbon dioxide, compared with the course of change in air at 10° C. In each case the continuous line indicates the calculated line of sucrose loss in air (see text).

EXPERIMENTS IN WHICH BRAMLEY'S SEEDLING APPLES WERE STORED AT 10° C. IN ATMOSPHERES OF (i) PURE OXYGEN, (ii) LESS THAN 0.5 PER CENT. OXYGEN (CYLINDER NITROGEN), (iii) 20 PER CENT. OXYGEN AND 10 PER CENT. CARBON DIOXIDE IN NITROGEN, AND (iv) AIR CONTAINING 1 PART IN 500 (BY VOLUME) OF ETHYLENE.

In pure oxygen and in air containing ethylene the changes in sucrose content which occur after gathering are not widely different from those which occur in air. The same formal construction can be applied to them, and the constants of rate of loss thus obtained are significantly the same as those obtained in air.

It is doubtful, however, whether this construction can be applied to apples in less than 0.5 per cent. oxygen or in 10 per cent. carbon dioxide. While 10 or more observations were made on the fruit stored in air during the first 12 days or so, during which starch was present (Experiment 2 (V)), no observation was made during this period on the fruit stored in less than 0.5 per cent. oxygen or in 10 per cent. carbon dioxide. The first observation of sucrose, after 12 days, was below the initial value in each case. It can be held, either that a rise in sucrose content followed by a fall has in fact occurred (although not recorded) during these 12 days, or that the sucrose content does under these conditions fall from the outset. If the latter assumption is made, rate-of-loss constants of 1.26 for fruit in 10 per cent. CO₂ and 0.371 for fruit stored in "nitrogen" are obtained, but the scatter of the

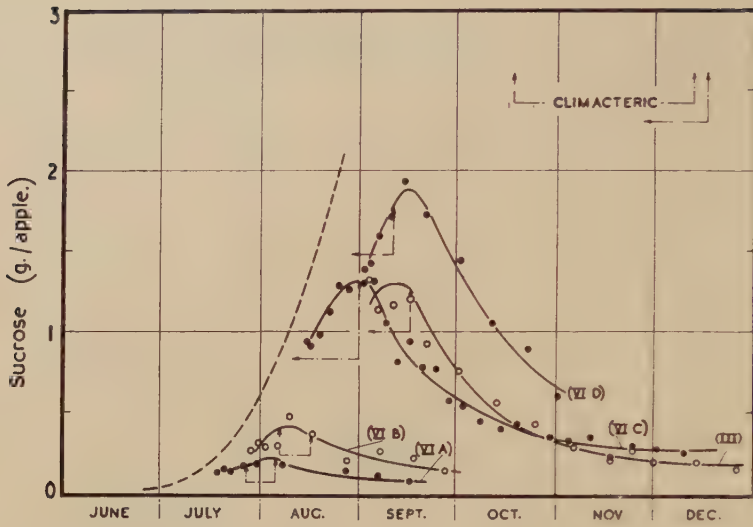


FIG. 12.

The accumulation of sucrose in Worcester Pearmain apples during growth (interrupted line), and the change in sucrose content during storage at 10° C. after gathering (continuous lines).

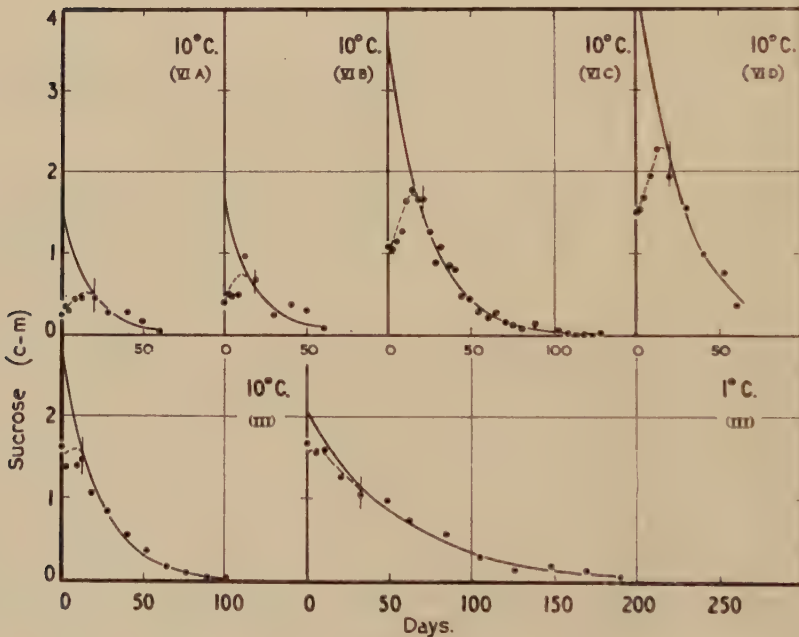


FIG. 13.

Logarithmic fall in sucrose content of Worcester Pearmain apples during storage at 10° C. and at 1° C. (see text). The vertical lines indicate the time at which starch has disappeared from the system.

observation points about the calculated line is very much wider than it is for fruit stored in air. In Figure 11 the first assumption is made. In this figure the scatter of the points is reasonably the same as in air, and we presume that a prolonged rise in sucrose content occurs, interrupting the usual logarithmic decline.

THE EXPERIMENTS WITH WORCESTER PEARMAIN APPLES.

Two experiments (III and VI) were carried out with Worcester Pearmain apples. In Experiment VI four gatherings (VI A, VI B, VI C and VI D) were made between 18th July and 2nd September, 1935, and the fruit was stored at 10° C. In Experiment III there was only one gathering, on 3rd September, 1931, and the fruit was stored at 10° C. and at 1° C. The data have been dealt with in the same way as those for the Bramley's Seedling apples described above, and they have been found to fit into a similar scheme (see Table II and Figures 12 and 13). The data for the third gathering in 1935 (VI C), which were the most complete, conform closely to the Bramley picture. In comparing the initial contents of starch, sucrose and glucose of the four gatherings of Experiment VI with those of Archbold's population of 1930, we find higher contents of starch associated with lower contents of sucrose and glucose.

There is slight evidence that the rate constants of sucrose loss and the final low level values may be higher for Worcester Pearmain than for Bramley's Seedling apples. In the one case observed the temperature coefficient of the rate constant of sucrose loss in Worcester Pearmain apples is the same as that for Bramley's Seedling apples.

SUMMARY

The pattern of behaviour of apples (Bramley's Seedling and Worcester Pearmain) as regards their sucrose content during growth and in storage is described, and a general formulation, which covers all the cases examined, is put forward.

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EXPERIMENTS ON THE CONTROL OF BROWN ROT OF APPLES AND PLUMS

II. WINTER SPRAYING TRIALS*

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THE object of the experiments described in this paper was to examine the possibility of controlling brown rot of apples and plums, caused by *Sclerotinia fructigena* Aderh. and Ruhl. and *Sclerotinia laxa* Aderh. and Ruhl., by the winter application of an eradicant fungicide. It was hoped that such a material would inhibit summer sporulation of overwintering sources of infection. This might result, in its turn, in a reduction of brown rot infection of the subsequent crop. Such a method of attack on the disease had received comparatively little study in the past, particularly in this country.

REVIEW OF THE LITERATURE.

Marsh (1947) recently obtained promising results in a preliminary trial at Long Ashton by winter application of a 0.3 per cent. phenyl mercury chloride preparation as an eradicant spray against brown rot of plum. He found that, in the following June, sporulation of the fungus in treated fruits was largely inhibited. Subsequently, Byrde (1949) showed that such a spray killed the mycelium of *S. fructigena* in the surface tissues of treated mummified apples, thus largely inhibiting spore pustule production. Further tests (Byrde, 1950) indicated that, to achieve 95 per cent. inhibition of sporulation, phenyl mercury chloride should be used at approximately 0.3 per cent.

Following earlier work on the use of arsenite eradicant sprays against *S. laxa* by Wilson (1942) and other workers, Byrde (1949, 1950) showed that monocalcium and sodium arsenite preparations were also effective eradicant fungicides against *S. fructigena* in mummified apples and plums.

Phytotoxicity was fairly widespread in American field trials with arsenite eradicant sprays, and this factor led Wilson (1943) to investigate the eradicant efficiency of other compounds. The chlorinated phenol derivatives appeared the most promising in extensive exploratory tests, and Wilson (1950) developed the use of sodium pentachlorophenate as an alternative to the arsenites. Although less phytotoxic, the material did not penetrate so effectively, and Wilson found that temperature and rainfall were factors governing its efficiency. Byrde (1950) examined the effect of the material on detached mummified plums infected with *S. fructigena*, and found that its eradicant efficiency was of the same order as that of phenyl mercury chloride and monocalcium arsenite. Sodium dinitro-*ortho*-cresolate also showed some promise.

None of the literature on eradicant sprays against the brown rot diseases refers

* The investigations published in this paper formed part of the work undertaken for the Degree of Doctor of Philosophy of the University of Reading. The trials were carried out at Long Ashton Research Station, by kind permission of the Director.

to the control of subsequent fruit infection, with which the present research is concerned. Most of the field work reviewed was carried out on *S. laxa*, and it is the blossom wilt and spur blight which is the serious phase of the disease caused by this species and on which all infection records were obtained. Furthermore, the data of field experiments carried out by workers on other species were confined to records of the suppression of sporulation of mummified fruits in preliminary trials, and notes on phytotoxicity. Thus no information is available from previous experimental work as to the likely effect of a good eradicant spray, which will largely inhibit pustule production, on the subsequent fruit infection. Horsfall (1945), however, in a general consideration of the use of eradicant sprays, gave a warning that they are often ineffective against pathogens having several generations in a year, as such fungi are able to build up rapidly from the few sources of infection that are bound to survive, so nullifying the effect of the eradicant treatment. *Sclerotinia fructigena* is an example of such a pathogen, particularly in its phase of apple fruit infection, which continues over a season of two or three months. The experiments described below showed, as will be seen, that the effect of eradicant sprays on this fungus followed the course of events predicted by Horsfall.

EXPERIMENTAL.

Trees.

Tests were carried out at Long Ashton on rows of 15-year-old bush apple trees of the variety Laxton's Superb, planted at 30 feet apart, and on 15-year-old standard plum trees of the variety Giant Prune, planted at 24 feet apart. In order to minimize the spread of disease from one treatment to another, the trees sprayed with a given fungicide were grouped in blocks throughout the field trials. Tests were also carried out on detached mummified plums of mixed varieties, infected with *S. fructigena* and *S. laxa*, and on detached cankered apple twigs infected with *S. fructigena*.

Fungicides.

The following materials were formulated as described in an earlier paper (Byrde, 1952):

Copper sulphate.

Phenyl mercury acetate (90 per cent. preparation).

Phenyl mercury formamide (3.3 per cent. preparation).

Phenyl mercury mono-ethanol ammonium acetate (as a water-miscible liquid containing 11.5 per cent. active material).

Diphenyl mercuric salt of di-2:2'-naphthyl methane-3:3'-disulphonic acid (10 per cent. preparation).

Sodium dinitro-*ortho*-cresolate.

Sodium pentachlorophenate.

8-Hydroxyquinoline sulphate.

The following materials were also tested:

(1) Phenyl mercury chloride. In these trials phenyl mercury chloride was compounded as a stock suspension by grinding together:

Phenyl mercury chloride	..	..	..	..	10 gm.
10 per cent. sulphite lye	..	..	..	..	100 ml.

(2) Pentachlorophenol. This was used in a stock tar-oil emulsion, prepared as follows:

Pentachlorophenol	..	..	..	..	..	9 gm.
Tar-oil	..	..	..	..	..	50 ml.
10 per cent. sulphite lye	..	..	..	..	..	50 ml.

The pentachlorophenol was first dissolved in the tar-oil by gentle warming, and the oily solution then emulsified.

Tests on detached mummified fruits and cankers: 1950.

These tests followed the general lines of the previous year's experiments, using a wider range of fungicides, which may be broadly classified under four headings:

- Organo-mercurials.
- Substituted phenols and cresols.
- 8-Hydroxyquinoline derivatives.
- Miscellaneous organic compounds.

The fungicides, with suitable wetting agents incorporated, were applied on 3rd-6th April, 1950, to batches of twenty-five detached mummified plums not previously treated with any spray material. One hundred untreated fruits served as controls.

Fruits were treated by dipping each for five seconds in a beaker of fungicide: they were then dried for twenty-four hours on cellulosed wire netting trays in the laboratory. The trays were subsequently placed on a rack structure in the open.

Although sporulation occurred during June, the pustules were washed away by heavy rains in early July, and efforts to induce further sporulation by removal of the fruits to a moist greenhouse on 11th September, 1950, were unsuccessful, owing to cold sunless weather. Fortunately, preliminary recordings of sporulation had been carried out during June, classifying the degree of pustule production of each treated batch of fruit into one of five categories (0 to 4). Table I shows the results obtained: the sporulation of control fruits was vigorous (Category 4).

These results show that an effective inhibition of pustule production in June followed the use of each of the fungicides listed, at a suitable concentration. The organo-mercurials appeared more effective at low concentrations than in previous years.

On 6th April, 1950, three of the fungicides, each at a single concentration with suitable wetting agents added, were also applied to detached brown rot cankers of apple, using eleven cankers per treatment, and twenty-two untreated cankers as controls. Preliminary recordings of pustule production made in June, 1950 showed that 0.8 per cent. sodium pentachlorophenate and 0.8 per cent. 8-hydroxyquinoline sulphate (followed by copper sulphate) largely inhibited pustule production while phenyl mercury chloride (at 0.2 per cent. Hg) did so to a lesser extent.

Fungicides ineffective as eradicants.

For convenience, the large number of fungicides proving unsatisfactory in preliminary trials throughout the three years of the research are listed separately below:

Tricalcium arsenite, 0.25%; pentachloronitrobenzene, 0.7%; tar-oil emulsion, 5.6%; copper naphthenate, 0.6%; copper sulphate, 5%; dichloronaphthaquinone

TABLE I.

Degree of pustule production of detached mummified plums in June, 1950.

Fungicide.	Fungicidal concentration.					
	0·8%	0·4%	0·2%	0·1%	0·05%	0·025%
Sodium dinitro- <i>ortho</i> -cresolate ..	0	1	2	3	—	—
Sodium pentachlorophenate ..	0	1	2	3	—	—
Pentachlorophenol (a) ..	0	0	1	2	—	—
8-Hydroxyquinoline sulphate (b) ..	0	0	1	3	—	—
Phenyl mercury chloride (c) ..	—	—	0	0	1	1
Phenyl mercury acetate (c) ..	—	—	0	0	0	1
Phenyl mercury acetate (c) (d) ..	—	—	0	0	0	1
Phenyl mercury formamide (c) ..	—	—	—	0	—	—
Phenyl mercury mono-ethanol ammonium acetate ..	—	—	—	0	—	—
Diphenyl mercuric salt of di-2:2'-naphthyl methane-3:3'-disulphonic acid (c) ..	—	—	—	0	—	—

NOTES: The categories of degree of sporulation are as follows:

0—None. 1—Trace. 2—Slight. 3—Moderate. 4—Vigorous.

(a) Concentrations expressed as equivalent concentrations of sodium pentachlorophenate.

(b) When dry, fruits treated with equivalent concentration of copper sulphate, without wetting agent.

(c) Concentrations expressed as % Hg. Phenyl mercury chloride contains 64% Hg.

(d) When dry, fruits treated with equivalent concentration of sodium chloride, together with wetting agent.

(50%), 1%; dinitro-*ortho*-cresol, 0·1%; glyoxalidine acetates (54%), 1%; *Bis* (2-hydroxy-5-chlorophenyl) sulphide, 0·8%; 8-hydroxyquinoline sulphate, 0·8%; malachite green, 0·4%; N-trichloromethylthio-tetrahydrophthalimide (50%), 0·8%; 1-(4-chlorophenyl)-3:5-dimethyl-4-nitroso-pyrazole, 0·1%; 1-phenyl-3:5-dimethyl-4-nitroso-pyrazole, 0·1%; dinitroacrylphenylcrotonate (25%), 0·4%.

Field spraying trials.

These trials were carried out to follow up the preliminary results with phenyl mercury chloride and, at the same time, to investigate the effects of the inhibition of sporulation of mummified fruits on the final crop infection.

Plum trial: 1950. Twelve Giant Prune plum trees, each bearing 10-17 mummified fruits, were used for this trial. Six trees were sprayed with 0·3 per cent. phenyl mercury chloride on 4th March, 1950, leaving the remaining six as controls.

A DDT spray ($\frac{1}{2}$ lb./100 gallons in a benzol-lye emulsion) was applied to all trees on 6th March, 1950, for the control of plum aphids.

On 1st September, 1950, batches of mummified fruits from treated and untreated trees were brought into the laboratory and incubated in a moist chamber for three days; pustule production of *S. laxa* and *S. fructigena* was then recorded and is shown in Table II.

The inhibition of pustule production resulting from the phenyl mercury chloride spray was thus of the order of 90 per cent.

Infection of the current season's crop was estimated on 31st August—1st September, 1950, from a sample of 250 fruits from each tree. In this count the number of damaged healthy fruits was recorded, and distinction made between

TABLE II.

Pustule production of mummified Giant Prune plums on 4th September, 1950.

Treatment.	No. of fruits examined.	No. bearing pustules.	Mean no. of pustules per fruit.
Phenyl mercury chloride 0.3%	17	6	4.53
Control	32	23	40.62

primary and secondary infections. By this means an estimate was made of the proportion of damaged fruits which had become infected.

Table III shows the results obtained.

Chi-square analysis of the data of columns (3) and (4) showed that in neither case was there a significant difference between sprayed and unsprayed trees.

Apple trial: 1949. A trial was carried out on forty-eight Laxton's Superb trees, planted in two rows, separated by six rows of Worcester Pearmain. Half of each row was sprayed; the remaining trees served as controls. Overwintering mummified fruits were present on the trees, in varying numbers.

The following fungicidal wash was applied on 1st March, 1949:

Phenyl mercury chloride	0.2%
Petroleum oil emulsion (JD-2)	3%
Wetter	0.25%

TABLE III.

Brown rot infection of Giant Prune plums on 31st August-1st September, 1950.

(1) Treatment.	(2) Tree no.	(3) Proportion of damaged fruits infected.	(4) Contact infections expressed as proportion of total infections.
Phenyl mercury chloride 0.3%	1	9/39	15/24
	2	3/23	3/6
	3	11/26	5/16
	4	4/17	0/4
	5	6/16	0/6
	6	4/13	2/6
	Total	37/134	25/62
Control	7	6/11	4/11
	8	13/27	2/5
	9	8/25	15/30
	10	15/43	7/15
	11	3/23	16/29
	12	7/22	8/14
	Total	52/151	52/104

The trees received a normal spring spray programme. On 21st July, 1949, mummified fruits were removed from four trees in each half-row, and pustule production estimated. Table IV shows the results of the count.

TABLE IV.

Pustule production of mummified Laxton's Superb apples on 21st July, 1949.

Treatment.	No. of fruits examined.	No. bearing pustules.	Mean no. of pustules per fruit.
Phenyl mercury chloride 0.2%	32	11	3.4
Control	35	35	63.6

It will be seen from these figures that the inhibition of pustule production resulting from the phenyl mercury chloride spray was of the order of 95 per cent.

Any fruits infected with brown rot were removed from the adjacent rows of Worcester Pearmain, to prevent them from acting as sources of infection to the trees in the trial. On 26th-30th September, 1949, fruit infection was recorded from samples of 250 fruits picked from each of the eight trees per half-row from which mummified fruits had not been removed earlier. Table V summarizes the results obtained.

TABLE V.

Brown rot infection of Laxton's Superb apples on 26th-30th September, 1949.

Treatment.	Half-row.	Mean % infection.
Phenyl mercury chloride 0.2%	1 (West)	2.20
	2 (East)	0.95
Control	1 (East)	0.90
	2 (West)	6.84

It was noticeable during the recording that wasp injury was very widespread in half-row 2 (West), and, to a lesser extent, in half-row 1 (West). It will be seen that there was no appreciable difference in infection between half-rows 1 (East) and 2 (East), where, in the absence of wasp attacks, comparison can fairly be made. No significant correlation was obtained between the number of overwintering fruits and subsequent crop infection on a given tree, either for unsprayed or sprayed blocks.

Phytotoxicity.

A feature of the winter spraying trials was the lack of damage to the trees when the fungicides were applied during dormancy; only when applications were delayed until bud burst was phytotoxicity observed (Byrde, 1949).

DISCUSSION.

GENERAL CONSIDERATIONS.

Clearly, the presence in the early summer of the overwintered sources of infection is of fundamental importance in the perpetuation of the brown rot fungus. In plums, this overwintering inoculum consists of infected mummified fruits: in apples, it comprises both mummified fruits and shoot cankers. Hand removal of mummies is laborious and often impracticable. An eradicant spray, in addition to its labour-saving action in dealing with mummified fruits, might also be effective against shoot cankers, which are probably frequently overlooked when hand treatments are carried out.

The final aim of the experiments with winter eradicant sprays was to explore the possibility of reducing brown rot attack on the current season's fruit crop by inhibiting sporulation on the overwintering infections. The work detailed in this paper shows that a 90 per cent. reduction of sporulation of mummified fruits is practicable but is not sufficient. Spore counts indicated that a mummified apple in early summer produced some 4,000,000 spores, so the action of the eradicant spray was to reduce this number to approximately 400,000. Such an inoculum is still sufficient to infect a few developing fruits that sustain skin injury. Each of the current-season fruits thus infected produces at least 10,000,000 spores, so that the infection potential of the newly-rotted fruits rapidly reaches a point at which it outweighs that of the overwintered mummies. The degree of sporulation on these mummified fruits then becomes relatively unimportant, and the occurrence of fruit injury determines the subsequent rate of spread of the disease.

The difficulty of obtaining a complete inhibition of sporulation by winter treatment is one inherent in all field spraying operations, namely the impossibility of ensuring complete coverage. Portions of mummified fruits may be so shielded by other fruits or by branches as to be unassailable by any spray application.

A further series of experiments appears justified, aiming at a greater inhibition of sporulation on a field scale, and investigating the effects of this on subsequent fruit infection. Should the results of these trials prove unsatisfactory, it can be concluded that winter spraying against brown rot is of little value.

Mention may be made of the results reported by other workers, who used eradicant fungicides against blossom wilt and twig blight infections. A reduction in sporulation of the order of 90 per cent. was often followed by an appreciable reduction in disease incidence, almost certainly because, in this form, the pathogen has but one or two generations in a year. There is thus little opportunity for the rapid build-up from small sources of inoculum (Horsfall, 1945; pp. 46-47).

MERITS AND DEMERITS OF PRINCIPAL ERADICANT FUNGICIDES TESTED.

Phenyl mercury chloride, a powerful fungicide, has proved fairly reliable in suppressing sporulation of mummified fruits. The necessity of obtaining thorough coverage when using phenyl mercury chloride sprays has been demonstrated (Byrde, 1949), and this is difficult to achieve in practice on a field scale. The present high cost of the compound is a serious practical disadvantage to its commercial use at effective concentrations for eradicant action.

Laboratory examination of treated mummified fruits indicates that, unlike phenyl mercury chloride, the arsenites possess penetrative properties (Byrde, 1949);

this has also been demonstrated by Palmiter and Keitt (1937) and by Wilson (1942). Thus, imperfect coverage of mummified fruits in field spraying is of less consequence than in using phenyl mercury chloride. Since the inhibition of sporulation of detached mummified fruits treated with arsenites was generally most promising, it is particularly regrettable that their highly poisonous nature prejudices their use on a large scale in this country.

Of the substituted cresols and phenols, both sodium dinitro-*ortho*-cresolate and sodium pentachlorophenate have shown some promise as eradicant fungicides in tests on detached mummified fruits but, unfortunately, as reported by Wilson (1943), they appear to be somewhat erratic in field performance, probably due to their high solubility and the consequent leaching effect of rain.

Pentachlorophenol, on the other hand, being virtually insoluble, should not suffer from this drawback, and is considered to be the most promising of all the eradicant fungicides tested, using detached mummified fruits. It is soluble in tar-oil, and could be used conveniently in a winter tar-oil emulsion, which itself may have some fungicidal effect. Although not appreciably soluble in petroleum oil, it might be possible to incorporate it in such an oil emulsion by means of a mutual solvent. It has the great merit of cheapness.

Further experiments are required to investigate the penetrative properties of the material and its performance on a field scale. Its principal disadvantage is that it is poisonous and needs to be handled with some care.

SUMMARY.

1. In trials on detached mummified plums infected with *Sclerotinia fructigena* and *S. laxa*, winter application of several eradicant fungicides largely inhibited the production of sporing pustules from these fruits, and from brown rot cankers on apple twigs. In general, the effective materials fell into three broad chemical groups—organo-mercurials, arsenites, and substituted phenols and cresols. Many fungicides of value as protectants against infection by air-borne spores showed no eradicant action on mycelium of the brown rot fungi in plant tissues.

2. Although field applications of phenyl mercury chloride at 0.2 per cent. or 0.3 per cent. in early March resulted in approximately 90 per cent. reduction in sporulation of overwintered mummified apples or plums borne on the trees, no significant control of the brown rot infection of the subsequent crops was achieved. This is mainly a result of the prolific and rapid sporulation of the pathogen, resulting in several generations during the summer, and a rapid build-up of the disease from a small inoculum.

3. Phytotoxicity was a negligible factor in the course of the winter spraying trials.

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LEAF CURL, A VIRUS DISEASE OF RASPBERRIES IN SCOTLAND

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DURING a visit to the raspberry districts of Eastern Scotland in 1941, Mr. N. H. Grubb discovered outbreaks of a serious leaf curling disease in plantations of the variety Norfolk Giant. The symptoms were described by Harris, Bryce and Foister (1943), who also reported the disease to be graft transmissible from Norfolk Giant to healthy plants of Baumforth's Seedling B. The symptoms on the latter variety were those of the so-called "Baumforth's disease" which was considered largely responsible for the disappearance of that variety from Scotland in the late 1920's. On further investigation, in 1944, the Leaf Curl disease proved to be widespread in Norfolk Giant in the Strathmore area of Angus and East Perthshire and, as that variety was then being planted extensively in the East of Scotland, the apparently rapid spread of this new and lethal disease threatened serious loss to the raspberry industry. Since 1944, the Leaf Curl disease has been recorded in East Lothian but has not yet been found in the raspberry growing areas of Fife and Lanarkshire, nor in England or Wales.

The work reported here has confirmed the virus nature of the disease and provided information on the reactions to infection of a number of raspberry varieties. In the field, Leaf Curl spreads more rapidly than any other known raspberry virus disease but the natural means of spread has not been discovered. The causal virus has not been transmitted by mechanical methods, other than grafting, and repeated attempts to transmit by means of the common raspberry aphids, *Amphorophora rubi* Kalt. and *Doralis (Aphis) idaei* V.d.G. have failed.

In the following account, this Norfolk Giant disease will be referred to as Leaf Curl and the causal virus as the Leaf Curl virus. These designations do not imply any identity or relationship of the virus with those causing the analogous American Leaf Curl diseases of raspberries as described by Bennett (1927, 1930).

FIELD SYMPTOMS ON NORFOLK GIANT

In the field, Leaf Curl-infected stools of Norfolk Giant are recognizable in early spring by the fruiting canes being either completely dead or producing a large proportion of distorted fruiting laterals. In extreme cases, the laterals are reduced to short rosetted growths of small, curled and brittle leaves that prematurely expose the flower buds, and they usually die. Less severely affected laterals grow out and produce flowers and fruit though the leaves are usually distorted by conspicuous yellow or necrotic blotches and the stems are abnormally thickened and brittle (Pl. I(a)).

Young canes growing from plants infected the previous season are stunted and produce glossy green leaves that are tightly down-curved; the leaves may,

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at times, show a varying amount of diffuse chlorosis (Pl. I(b)). The canes, leaves and petioles are extremely brittle and readily snap off when touched. These abnormalities are associated with necrosis of the phloem and collapse of the parenchymatous bark tissue. The young canes become necrotic at the tips towards the end of the season and die back to the basal buds (Pl. I(c)). The entire plant commonly dies during the following winter but may survive to produce a crop of stunted and curled canes the following season.

EXPERIMENTAL RESULTS.

TRANSMISSION BY GRAFTING.

Owing to the necrotic effects of the Leaf Curl virus, it has been extremely difficult to obtain successful graft unions between canes (scions) of infected Norfolk Giant plants and canes of healthy plants. In the experiments of 1942-45, healthy plants in pots were plunged alongside Leaf Curl-infected stools in the field; healthy and diseased canes were inarch-grafted *in situ* and, after union had been effected, the potted plants were transported to the glasshouse for observation.

Patch grafting of healthy canes with diseased material was also used successfully by one of us (R.V.H.) in an experiment at East Malling. In recent years the bottle grafting technique (Cadman, 1951a) has been used exclusively but it proved reliable only when scions of varieties tolerant to Leaf Curl were used.

Many individual experiments have been made over a long period and in the Table are brought together only those data which determine the distinctive features of the disease.

NORFOLK GIANT.

During 1944-46, 21 plants of Norfolk Giant (East Malling L234 clone) were grafted, in late June to July, to Leaf Curl-infected plants of the same variety. No symptoms were seen on any of these in the year of grafting, but six plants developed typical Leaf Curl symptoms in the subsequent year. The remaining 15 grafts failed to take and the indicators showed no symptoms.

On 13th May, 1947, three Norfolk Giant plants were bottle-grafted in the glasshouse with Leaf Curl infected Norfolk Giant scions, and conspicuous yellow blotches appeared on the young leaves of one of these by 12th July. No additional symptoms were noted until spring 1948, when the plants showed symptoms of chronic Leaf Curl. No symptoms developed on the other two plants. A similar experiment was made on 9th May, 1949, when five Norfolk Giant plants were grafted with scions from Leaf Curl-infected plants of Malling Promise. Blotching symptoms were noted on one of the indicators on 12th July and on a second plant on 9th August. These and two additional plants showed chronic Leaf Curl symptoms in May, 1950. The graft failed to take on the fifth plant and no symptoms developed.

These results indicate that the disease commonly has a long incubation period, and that the development of symptoms in the season of inoculation implies that the latter has occurred at the beginning of the growth period. It is probably significant that, in the field, newly infected plants are rarely found after mid-July, though plants recorded after this date as healthy may show chronic Leaf Curl in the succeeding spring. For this reason, grubbing of visibly infected stools has been found of limited use in controlling the disease in fruiting plantations.

BAUMFORTH'S SEEDLING B.

In July, 1942, canes of Leaf Curl-infected Norfolk Giant in a plantation in the Strathmore district of Scotland were inarched to four healthy potted plants of Baumforth's B. Two similar plants, exposed to infection but ungrafted, served as controls. All six plants appeared healthy on their removal to East Malling two months later, where they were kept under observation in a glasshouse until July, 1944. Neither of the two control plants showed any symptoms throughout this period. All four of the grafted plants, however, developed symptoms of chronic Leaf Curl by early July, 1943. The symptoms were very similar to those on Norfolk Giant already described, and three of the four plants were dead by July, 1944. During the summer of 1943, masking of symptoms was noted, a phenomenon characteristic of this disease and discussed below (page 205).

At Dundee, five plants of Baumforth's B grafted in the glasshouse on 13th May, 1949, with scions from infected Malling Promise plants developed severe Leaf Curl symptoms by 12th July. Masking of symptoms on leaves produced during warm weather was noted. Two plants were dead by spring, 1950, and the remaining three produced severely stunted canes with curled and brittle leaves.

The symptoms on the 1942 and 1949 indicator plants matched closely the available descriptions and photographs of the "Baumforth's disease" that was known "to be prevalent throughout the raspberry districts of Perthshire and Forfarshire" in the early 1920's (Grubb, 1923). At that time the disease appeared to be restricted to Baumforth's Seedling B and was not recorded, or at least not recognized, in plantations of Mitchell's Seedling, Devon, Red and Black Antwerp, Suplative or Lloyd George (McIntosh, 1926).

LLOYD GEORGE.

During 1944-48, over forty plants of this variety were grafted to infected Norfolk Giant plants but no evidence of transmission of the Leaf Curl virus was obtained. On 27th May, 1949, five Lloyd George plants (New Zealand stock) were bottle-grafted in the glasshouse with scions from infected Malling Promise plants. Slight chlorotic banding of the marginal leaf veins was noticed on the young leaves of two of the indicators on 16th August. In spring, 1950, these two and a third plant showed symptoms of a type hitherto unknown on Lloyd George. The young canes were stunted, compared with those on ungrafted control plants, but were not brittle. The leaves were not noticeably down-curved but showed a conspicuous veinbanding chlorosis resembling, though distinct from, that caused by the veinbanding virus (Cadman and Harris, 1951) (=Mosaic 1 disease, Harris, 1940). At the leaf margins, the main veins were bordered by narrow bands of chlorotic tissue whilst, in the body of the leaf, the intervenal tissue showed a general and patchy chlorosis (Pl. I(c)). The canes on these three plants matured normally in autumn, 1950, and showed no signs of necrosis.

Scions from these three plants were grafted in August, 1949, to three healthy plants of Norfolk Giant but no symptoms developed on the latter in 1950. This test was repeated in 1950 but the results are not available at the time of writing. It cannot, therefore, safely be concluded that the peculiar symptoms on the Lloyd George plants were caused by the Leaf Curl virus. On the remaining two plants of the set, the grafts failed to take and no symptoms developed.

In view of these results, earlier statements by the authors (Harris and Cadman, 1947; Anon., 1949) to the effect that Lloyd George behaves as a symptomless carrier of the Leaf Curl virus must be treated with reserve. The symptoms described above have not yet been found in the field and none of fifty canes dug from degenerate plants of Lloyd George growing in close proximity to Leaf Curl outbreaks in Norfolk Giant proved, on graft test, to be infected with Leaf Curl virus.

ST. WALFRIED.

The results of experiments with this variety in the years 1944-48 were difficult to interpret, for it was not then known that St. Walfried shows mosaic symptoms when infected with the Leaf Mottle and Yellows viruses (Cadman and Harris, 1951), frequently or invariably present with the Leaf Curl virus in infected Norfolk Giant stocks, a complication that does not affect the diagnosis of symptoms on the three varieties already considered. Also the stocks of St. Walfried used were themselves substantially infected with Mosaic 2 diseases (Harris, 1940), of which this variety is a symptomless carrier (Cadman, 1951b).

During the years mentioned, twenty-five St. Walfried plants were grafted to infected Norfolk Giant and transmission of Leaf Curl virus to seven of these was confirmed by a test graft to healthy Norfolk Giant plants. Compared with ungrafted control plants, cane growth on the infected plants was stunted and the leaves showed an inconspicuous intervenal blotching, but neither canes nor leaves were brittle and the latter only slightly down-curved. As the infected plants from the 1944 experiments were grown on for five years, infection is evidently not lethal.

In the field, similar symptoms were found, in 1945, on two St. Walfried plants near to an outbreak of Leaf Curl in a Norfolk Giant plantation. On graft testing to Norfolk Giant, both plants proved to be infected with Leaf Curl.

On 23rd June, 1950, five plants of a St. Walfried stock, infected only with an unidentified latent mosaic virus (Cadman and Harris, 1951) were grafted with scions from Leaf Curl-infected Malling Promise plants. The graft to one plant failed; the other four indicators all developed conspicuous chlorotic blotches on the leaves by 24th July. Growth of the young canes was stunted and the apices became necrotic. In spring, 1951, the fruiting canes on these plants were dead; the young canes were dwarfed and their leaves curled and distorted by conspicuous chlorotic spots. The Malling Promise source plants were known to be free from Mosaic 2 diseases but may have been infected with Leaf Mottle and Yellows viruses in addition to Leaf Curl. Diagnostic symptoms of Leaf Curl infection on St. Walfried have not, therefore, yet been accurately determined.

OTHER VARIETIES.

Attempts have been made to transmit the Leaf Curl virus by grafting to a wide range of European and N. American raspberry varieties and *Rubus* spp. but with little success. Apart from the difficulty of obtaining graft unions, the presence, in the stocks used, of other viruses to which Norfolk Giant is sensitive ruled out the possibility of using this variety as an indicator for confirmation of transmission of Leaf Curl. The results so far obtained are summarized in the Table and may be considered in two groups, corresponding to the parentage of the varieties.

(1) Infected scions of Norfolk Giant were grafted in 1945 to three plants of

Malling Promise known to be free from Mosaic 2 disease, and transmission of Leaf Curl virus to two of these was confirmed by a test graft to Norfolk Giant in 1948. In 1948 and subsequent years these two plants showed a diffuse chlorotic mottling of the leaves, the chlorosis sometimes appearing as an indistinct banding of the main veins (Pl. II(a)). The leaves showed no signs of curling or brittleness and the canes, though somewhat stunted, matured normally each season. Similar symptoms were found in 1947 on plants of Malling Promise close to a large outbreak of Leaf Curl in the Blairgowrie district and the presence of Leaf Curl virus in one of these was confirmed by a test graft to Norfolk Giant in 1948. The plants had an unthrifty appearance and the foliage, on both fruiting and young canes, a marked yellowish cast. It can, therefore, be concluded that Leaf Curl infection is not lethal to Malling Promise.

In 1950, closely similar symptoms developed on five plants each of Malling Exploit and Malling Seedling Z, sister seedlings of Malling Promise, grafted in 1949 with scions from the two Malling Promise plants described above. Transmission of Leaf Curl virus to at least one plant of each set has since been confirmed by a test graft to Malling Jewel.

(2) Scions from the infected Malling Promise plants were also grafted, in 1949, to five plants each of the Malling varieties Enterprise, Jewel and Notable. Conspicuous chlorotic blotches developed on the young leaves of two plants of Malling Jewel and one of Malling Notable four weeks after grafting. In spring, 1950, all three sets of plants showed severe symptoms characterized by brilliant yellow blotching on the leaves of the fruiting and young canes; thereafter, the three varieties differed somewhat in behaviour (Pl. II(b) and (c)). On the five plants of Malling Enterprise, leaves produced later in the season showed only a diffuse inter-venal mottle. This, together with slight stunting of the canes, was the only sign of infection. The leaves on the young canes of the Malling Jewel plants continued to show conspicuous blotching and veinbanding symptoms throughout the season and the leaves were markedly down-curved. Of the five Malling Notable plants, one was dead by spring, 1950; the young canes on the remaining four plants were severely stunted and brittle, the growing points necrotic and the leaves heavily marked with large chlorotic blotches throughout the season.

In 1947, symptoms similar to those just described were found in plantations of Malling Enterprise and Malling Notable adjacent to an extensive outbreak of Leaf Curl in Norfolk Giant and it was evident that, in the field, infection is rapidly lethal to these two varieties.

In their reactions to infection, the three Malling varieties, Enterprise, Jewel and Notable, closely resemble their common parent variety Preussen, which, in 1945, had been found to develop a lethal leaf blotching disease when infected with Leaf Curl.

MASKING OF LEAF CURL SYMPTOMS.

As reported above, the four plants of Baumforth's B grafted to Leaf Curl-infected Norfolk Giant in Scotland, in 1942, were removed to East Malling in September of that year and kept under observation in the glasshouse until July, 1944. During July, 1943, it was noticed that Leaf Curl symptoms diminished markedly in intensity on a proportion of the young canes produced by all four plants, some of these canes being indistinguishable in appearance from those of the

ungrafted control plants. However, all canes on the grafted plants showed symptoms of a severe attack of Leaf Curl in September and October of that year and by July, 1944, three of the plants were dead and the survivor showed slight Leaf Curl symptoms. Masking of symptoms was also observed on ten infected plants of Norfolk Giant grown in an unheated glasshouse at Dundee during the summer months of 1946, though all these plants again showed chronic Leaf Curl symptoms in spring, 1947. In May, 1946, shoots, apparently free from symptoms, were cut from these infected plants and bottle-grafted to three healthy plants of Norfolk Giant. One of the latter developed Leaf Curl in 1946 and 1947, showing that the virus was present in at least one of the apparently healthy shoots.

During the warm summer months of 1945 and 1947, transient masking of symptoms was noticed on infected plants of Norfolk Giant in the field. Leaves expanding and maturing during hot, sunny spells remained markedly less curled and brittle for the rest of the season. With the onset of cooler conditions, the new foliage resumed the typical curled and brittle state.

Experiments to determine the conditions under which masking occurs were begun in 1949 and 1950 and are not yet complete. Masking occurs at or above temperatures of 65-66° F. and response to variations in temperature is more marked in plants grown in partial shade. Leaves apparently remain capable of responding to variations in temperature only when actively expanding. Under certain conditions, leaves on infected plants may be indistinguishable in shape and poise from comparable leaves on healthy plants but the former have not been observed completely free from chlorotic symptoms of some description (Pl. II(d)).

FIELD SPREAD OF LEAF CURL.

Since 1945, six outbreaks of Leaf Curl disease in Norfolk Giant have been carefully surveyed as part of a programme designed to discover the means of spread and the primary sources of infection. Neither object has been achieved though the surveys have established the following facts:

Occasionally, outbreaks may develop on a large scale quite suddenly. In one outstanding case, almost every stool in a three-acre block of Norfolk Giant developed Leaf Curl in spring, 1948, although no infected plants had been noticed in the previous season. The disease has often appeared in stocks known, from their previous history, to be free from infection, and in plantations remote from other commercial stocks and varieties. Leaf Curl symptoms have never been observed on wild raspberries, usually abundant in the neighbourhood of commercial plantations, nor has the virus been detected, by graft test, in these or other wild *Rubus* spp. In only one instance has a source of infection for an outbreak been traceable to an infected stock of a Leaf Curl-tolerant variety and even this source was of doubtful significance.

Once the disease is established in a plantation of Norfolk Giant it appears to spread slowly, the number of infected plants approximately doubling itself every year. This rate is, however, much more rapid than that determined for certain other raspberry viruses in Norfolk Giant (Cadman, unpublished). Diagram 1 represents the records made in 1945 and 1948 of the numbers and positions of Leaf Curl-infected stools in a section of a Norfolk Giant plantation in the Forfar district. The area surveyed was approximately 42 × 86 yards, in which the individual stools were spaced 30 inches apart in rows 6 feet apart. Application of Van der Plank's

TABLE.
Results of graft transmissions of Leaf Curl virus to raspberry varieties.

Indicator host.	Date of grafting.	No. of plants grafted.	Infector source.	SYMPTOMS.			Leaf Curl detected in check test. No. of plants.
				(a) in current year.	No. of plants.	(b) subsequent year.	
Norfolk Giant	1944-46	21	Norfolk Giant	No symptoms	21	Necrosis and leaf curling	6
"	1947	3	"	Leaf blotching	1	"	1
"	1949	5	M. Promise	"	2	"	4
Baumforth's B.	1942	4	Norfolk Giant	No symptoms	4	"	4
"	1949	5	M. Promise	Leaf curling	5	"	5
Lloyd George	1949	5	"	Veinbanding	2	Severe chlorosis	3
St. Walfried	1944-48	25	Norfolk Giant	Chlorosis	2	Chlorosis	10
"	1950	5	M. Promise	Necrosis and leaf blotching	5	—	—
M. Promise	1947	3	Norfolk Giant	No symptoms	3	Chlorosis	2
M. Exploit	1949	5	M. Promise	"	5	"	1
M. Seedling Z	1949	5	"	"	5	"	1
Preussen	1945	1	Norfolk Giant	Leaf blotching	1	Necrosis and leaf blotching	1
M. Enterprise	1949	5	M. Promise	No symptoms	5	Severe blotching	1
M. Jewel	1949	5	"	Leaf blotching	2	Severe blotching and leaf curling	5
M. Notable	1947	1	Norfolk Giant	No symptoms	1	Severe blotching and necrosis	1
"	1949	5	M. Promise	Leaf blotching	1	{ Severe blotching and necrosis Dead	4
							1

(1946) test to these data shows that this pattern of spread must involve a certain amount of plant to plant spread of the disease.

As there is evidence that the virus is not spread by mechanical means, other than grafting, or through the soil, it is concluded that an insect vector exists. Periodic surveys of the insect fauna associated with Leaf Curl-infected plantations were made in the years 1944-46 but revealed no obvious correlation of disease spread with the incidence of possible vector species.

The aphids, *Amphorophora rubi* Kalt. and *Doralis (Aphis) idaei* V.d.G. have, elsewhere, been shown to be vectors of certain raspberry viruses (Cadman and Hill, 1947) but attempts to transmit the Leaf Curl virus by means of them have consistently failed, and it is now concluded that these species are not vectors of Leaf Curl. The experiments included transfers of large numbers of aphids from infected

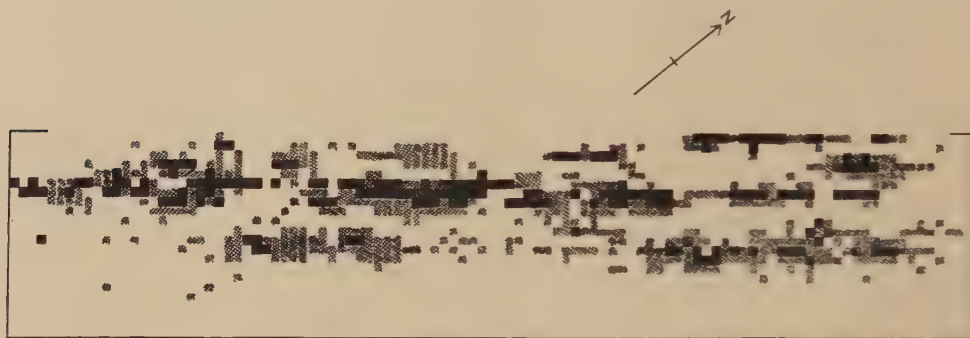


DIAGRAM I.

Map showing distribution and spread of Leaf Curl in a Norfolk Giant plantation.

- = infected plants recorded in 1945.
- ▨ = infected plants recorded in 1948.

Norfolk Giant plants in the field to healthy plants of Norfolk Giant and Malling Jewel in the glasshouse; mass transfers and assisted migrations of aphids from Leaf Curl infectors to healthy plants of Norfolk Giant grown in gauze-covered cages outdoors; and controlled feeding experiments in which aphids were given various feeding periods on infected plants before transfer, in large numbers, to healthy test plants. The results of experiments with certain *Jassid* and *Capsid* species were also negative. Species of the former group found on raspberries are mostly migrants from surrounding trees and the phytophagous *Capsid* species have a damaging mode of feeding. It is, therefore, thought unlikely that any of these insects are vectors. *Thrips* species, of which a number are common on raspberries, have not yet been fully investigated.

The indications of plant to plant spread of Leaf Curl, provided by the map records, imply that the vector must, for a time at least, be capable of living and feeding on raspberries.

DISCUSSION.

The grafting experiments described above, though establishing the virus origin of the Leaf Curl disease, are incapable of showing whether only one virus is concerned.

PLATE I.



a



d



b



c

(a)-(c). Symptoms of Leaf Curl on Norfolk Giant.

- (a) Initial leaf blotch symptom.
- (b) Chronic symptoms on young canes.
- (c) Necrosis of young canes.

(d). Suspected Leaf Curl symptoms on Lloyd George.

PLATE II.



(a)-(c). Leaf Curl symptoms on Malling Promise, Malling Jewel, and Malling Notable respectively.
(d). Zonation of Leaf Curl symptoms on Norfolk Giant in response to variations in temperature.
Zones of normal leaves mark periods of high temperature.

In the absence of evidence to the contrary, it is concluded, however, that this is the case and that one and the same virus has been studied throughout this work. The experiments have shown that raspberry varieties differ considerably, one from another, in their reactions to infection. These differences are held to be due to genetical differences between varieties and not to variations in the inoculum used or to interaction between the Leaf Curl virus and other viruses present in the indicator stocks.

Compared with other raspberry viruses known in Britain, the most marked peculiarities of the Leaf Curl virus are its more rapid rate of spread in the variety Norfolk Giant in the field, and the fact that it has not, so far, proved transmissible by means of the aphids *Amphorophora rubi* Kalt. or *Doralis idaei* V.d.G.

The symptoms of Leaf Curl infection on Norfolk Giant and Baumforth's B are analogous, in some respects, to those of the Leaf Curl and Yellow Blotch-curl diseases of N. American varieties described by Bennett (1927, 1930, 1932) and Chamberlain (1938) respectively. Attempts, at Dundee, to obtain comparative data by transmitting the Leaf Curl virus to the American varieties Cuthbert, Herbert and Viking have consistently failed. Harris (1935) found that Lloyd George succumbed quickly to American Leaf Curl disease, transferred by patch grafting from infected Cuthbert plants. It is, however, not clear whether this reaction was caused by the Leaf Curl virus alone, by a combination of viruses present in the Cuthbert plants, or by a combination of either of these with viruses already present in the Lloyd George test plants. The symptoms on Lloyd George described earlier in this paper are different from those on Lloyd George described by Harris (1935) and Chamberlain (1938). It is, therefore, provisionally concluded that the α and β Leaf Curl diseases of Bennett (1930) and the Yellow Blotch-curl disease of Chamberlain (1938) are aetiologically distinct from the Leaf Curl disease described in this paper. The latter must also be considered distinct from Curly Dwarf (Prentice and Harris, 1950) which, although causing leaf curling symptoms on Baumforth's B, does not induce lethal blotching symptoms on either Baumforth's B or Norfolk Giant. The data do not exclude the possibility that some or all of the above-mentioned viruses may be related strains.

Leaf Curl has not yet been found outside Central Scotland and the reason for this restricted distribution is still obscure. There has, for many years, been a considerable traffic in raspberry stocks from Scotland to areas south of the border, and it is unlikely that, in the past, any great discrimination in the health of such stocks has been exercised. However, Leaf Curl-infected canes of varieties, such as Norfolk Giant, to which the disease is lethal, rarely establish themselves successfully. The distribution of the disease among old stocks of Lloyd George is unknown, so that the significance of the latter, as a vehicle of infection, cannot yet be assessed.

Masking of symptoms has not proved to be permanent under Scottish conditions, and typical Leaf Curl symptoms remained visible throughout the 1950 season on infected stools of Norfolk Giant grown in the south of England. Experiments are in progress to determine whether the virus is inactivated *in vivo* by high temperatures. Even should this prove to be the case, it is problematic whether climatic differences between Central Scotland and areas south of it are sufficiently distinct adequately to account for the apparent absence of the disease from the latter.

SUMMARY.

The symptoms of a necrotic, leaf-curling disease of Norfolk Giant raspberry, so far recorded only in Central Scotland, are described. The disease is shown to be graft transmissible. The disease is believed to be ætiologically distinct from the analogous N. American Leaf Curl and Yellow Blotch-curl diseases, and the names raspberry Leaf Curl disease and raspberry Leaf Curl virus are provisionally proposed for the disease and the causal virus respectively.

The Leaf Curl virus has been transmitted by grafting to a number of raspberry varieties and seedlings, and found to cause a necrotic leaf curling disease of Baumforth's Seedling B, a lethal yellow blotch disease of Preussen and the Malling varieties Enterprise, Jewel, and Notable, and a non-lethal chlorosis of Lloyd George, St. Walfried and Malling Promise. Temporary masking of symptoms on Norfolk Giant and Baumforth's B under warm weather conditions has been observed.

From records of the development of Leaf Curl outbreaks in Norfolk Giant plantations, it is concluded that the virus spreads more rapidly than others known to infect this variety, though no insect vector has yet been found.

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A LETHAL VIRUS DISEASE OF LLOYD GEORGE RASPBERRY IN SCOTLAND

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In 1943 and 1944, widespread death and failure of canes, associated with leaf blotching symptoms, were found in plantations of Lloyd George on two farms in the Coupar Angus district of Perthshire. No further cases have been recorded and, with the ploughing up of the affected plantations, the disease has not since recurred.

The experiments reported here show that the disease is graft transmissible and ætiologically distinct from the Leaf Curl disease described in an earlier publication (Cadman and Harris, 1952), and the name Yellow Blotch is proposed. No insect vector has been identified.

FIELD SYMPTOMS.

Affected plants of Lloyd George showed necrosis of the fruiting canes and the young canes were stunted and showed coarse, circular or irregular yellow blotches on the lower leaves (Pl. I(a)). The leaves were not markedly down-curved and symptoms were masked on foliage produced during the summer months, reappearing on leaves produced in late August and September. Infected plants rarely survived for more than one growing season.

Closely similar symptoms were found on plants of Burnetholm Seedling growing near one of the affected areas of Lloyd George.

EXPERIMENTAL RESULTS.

In 1943, four mosaic-free plants of Lloyd George were grafted *in situ* to Yellow Blotch-infected canes. No symptoms developed on these or on four ungrafted control plants up to the time they were discarded in 1945 and 1946. Of four healthy plants of Norfolk Giant, also grafted in 1943 to similar material, two developed symptoms, in 1944, of a mixed virus infection including Mosaic 2 disease, and two showed symptoms of a new and distinct type. Four ungrafted control plants remained healthy.

Leaf symptoms on the two exceptional plants consisted of small, irregularly shaped and distributed, intervenal chlorotic spots, the leaves being slightly down-curved (Pl. I(b)). This disease was transmitted by grafting to a further three Norfolk Giant plants in 1944 and 1945. The latter were in turn grafted in 1946 to three plants of a vigorous commercial stock of Lloyd George; two of these died before spring, 1947, whilst the third showed Yellow Blotch symptoms in 1947 and 1948. That the Mosaic 2 and other diseases initially present in the indicators were not essential components of Yellow Blotch was shown by an experiment in 1947. Two plants of Lloyd George (from a Scottish source) free from Mosaic 2 and Yellow diseases (Cadman and Harris, 1951) developed Yellow Blotch symptoms when grafted with infected Norfolk Giant.

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Necrosis of canes and severe chlorotic leaf blotching, similar to that observed in the field in 1943, developed on two of five plants of Burnetholm Seedling grafted in 1949 with infected Norfolk Giant scions (Pl. I(c)).

The disease was also transmitted, by grafting, from Norfolk Giant to plants of Baumforth's Seedling B, St. Walfried and Malling Promise, as shown in the Table. The first two varieties developed severe intervenal chlorotic spotting; the leaves were markedly down-curved and brittle and the canes stunted compared with ungrafted control plants. The infected plants of Malling Promise were dwarfed and the leaves showed an indistinct and general chlorosis but were not curled. Infection is evidently not lethal to any of these varieties as the plants graft-infected in 1946 and 1948 are still alive.

TABLE.

Results of graft transmissions of Yellow Blotch disease.

Indicator.	No. of plants.	Infector.	Year of graft.	Yellow Blotch.	No symptoms.	Yellow Blotch in check tests.
Lloyd George	4	Lloyd George	1943	—	4	—
"	4	Controls	1943	—	4	—
"	3	Norfolk Giant	1946	3	—	—
"	2	"	1946	2	—	—
Norfolk Giant	4	Lloyd George	1943	2	2	2/2
"	3	Norfolk Giant	1944, 45	3	—	3/3
Burnetholm Seedling	5	"	1949	2	3	—
Baumforth's B	2	"	1946	2	—	—
St. Walfried	2	"	1946	2	—	—
Malling Promise	3	"	1948	2	1	1/2
Cuthbert	2	"	1946	—	2	0/2
"	5	"	1949	—	5	—

In contrast with the behaviour of infected Lloyd George, there was no noticeable masking of symptoms during hot weather on any of the infected Norfolk Giant, Baumforth's B, St. Walfried and Malling Promise plants.

Two attempts were made to infect plants of the N. American variety Cuthbert but no confirmation of transmission of Yellow Blotch was obtained.

In 1947, colonies of the aphids *Amphorophora rubi* Kalt. and *Doralis* (*Aphis*) *idaei* V.d.G., reared on healthy plants of Norfolk Giant, were transferred to plants of Lloyd George and Norfolk Giant infected with Yellow Blotch. After an infection feeding period of three weeks, large numbers (c. 1,000) of aphids were transferred from the source plants to each of nine Lloyd George test plants. Six of these received *A. rubi* and three *D. idaei*. No symptoms developed on any of the test plants.

CONCLUSIONS.

It is concluded from these results that Yellow Blotch is a virus disease and, in the absence of contrary evidence, the disease is presumed to be caused by one virus. Though this virus produces symptoms on Norfolk Giant and Lloyd George distinct from any so far described on these varieties in Britain, the data do not exclude the possibility that the Yellow Blotch virus is related to other known raspberry viruses.

The leaf and cane symptoms on infected Lloyd George and Burnetholm Seedling closely resemble those of the N. American Yellow Blotch-curl disease on Lloyd George, Cuthbert and other N. American varieties described by Chamberlain (1938). In the absence of comparative data, the two diseases must, at present, be considered ætiologically distinct.

SUMMARY.

A lethal leaf blotching disease of Lloyd George and Burnetholm Seedling raspberries in Scotland is shown to be graft transmissible. The causal virus produces mosaic symptoms of a hitherto unrecorded type on Norfolk Giant, and non-lethal leaf curling and mosaic diseases on Baumforth's Seedling B, St. Walfried and Malling Promise. No insect vector has been discovered.* The disease resembles, in some respects, the N. American Yellow Blotch-curl and the provisional name Yellow Blotch is proposed.

ACKNOWLEDGMENTS.

Our thanks are due to Mr. A. D. Bryce, Edinburgh and East of Scotland College of Agriculture, for bringing this disease to our notice and for valuable help in the initial experiments. Acknowledgment is also made to the Agricultural Research Council who have financed the work of which this forms a part.

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NOTE ADDED IN PROOF.

It has since been found that the Yellow Blotch virus is transmitted by *Amphorophora rubi* but not by *Doralis idaei*.

* See note added in proof.

PLATE I.



(a) and (b). Yellow Blotch symptoms on naturally infected plants of Lloyd George (Fig. a) and Burnetholm Seedling (Fig. b) in the field.

(c). Norfolk Giant graft infected with Yellow Blotch virus.

REVIEWS

PLANT EMBRYOLOGY—EMBRYOGENY OF THE SPERMATOPHYTA. By D. A. Johansen. (Wm. Dawson & Sons, Ltd., London; The Chronica Botanica Co., Waltham, Mass., U.S.A., 1950, pp. 323, illus. Price U.S. \$6 or special edition \$14.)

Gradually the less appreciated aspects of botany are being revised and monographed. This work is an example, and is published in excellent format by the Company which is doing so much to lay the foundations for future "International Plant Science". The subject is neglected because plants have apical meristems which take away from the plant-embryo that finality which enshrines the animal. Many must have felt, however, the gap but lamely filled in general botany by *Capsella* and *Alisma*. We opened this monograph with enthusiasm, we have been impressed by the detail, but we are unhappy.

The subject is restricted to the early growth of the zygote up to the state of differentiation of shoot and root and of inception of their tissues. Full-grown embryos, as we all behold them in ripe seeds, are omitted. A huge subject of great taxonomic importance is unmentioned, and where is it to come in? There is no account of the complete embryogeny of any plant, how cotyledons grow and fold, radicles double up, curvatures arise, or the new-born meets the world. The author is concerned with cell-lineages. If Maheshwari's conception of embryology errs on the generous side, this seems to us misleadingly narrow.

The author sets out in great detail, and in taxonomic order, this early embryology of the Gymnosperms and Angiosperms, appending the necessary references to each family or order, and indicating which have not been studied. For the specialist, without a really large library, this information will be invaluable and so we can thoroughly recommend the book. What disappoints us is the little that the general botanist can derive. Thus, the author lays down that unification of the Gymnosperms is artificial. They are treated as four phyla, without embryological synthesis; but, on comparing Figs. 2-35 (Gymnosperms) with the remainder (Angiosperms), the reader perceives a "Gymnospermous facies", if only because their embryos appear upside down. What we have learnt is that the author's attitude to the Gymnosperms is not borne out by his exposition.

For the Angiosperms the author has written two, very difficult, synthetic chapters. In one he lays down his "embryonomy", or laws of embryogeny, and develops an equational representation for cell-lineages. Without diagrams, it is extremely hard to follow what these laws mean: they are called fundamental, but the author entirely overlooks the biophysical side of cell-division and cell-lineage, so well explained by D'Arcy Thompson. Thus, Figs. 36-80 are typifications of D'Arcy Thompson's laws, and we feel that this oversight is responsible for the rather old-fashioned didacticism. The equational terminology seems so confused as to be unacceptable. The author uses *co* for the root-cap and insists on *cot* for the cotyledon: then he uses *pco* for the cotyledonary region. For the central cylinder of root and stem he uses *iec* and *icc* respectively; then, he uses *iec'* for the stem-cortex. In Fig. 40 (*Capsella*), the reader must puzzle out why *m*, *n*, *o*, and *p* become *d*, *f*, *g*, and *y*. Here was a great opportunity for introducing an internationally acceptable symbolism. In the second synthetic chapter, the author classifies the ways of

Angiosperm embryogeny, employing six types and many variants. He discards the system of Souèges as demanding too much detail in following cell-lineage, but the variations of the author's Asterad type seem to us the return of the boomerang. Both classifications appear to be without taxonomic use.

Finally there are three chapters on apomictic and adventitious embryos and polyembryony, and a necessary glossary. Analytic tabulation of the terminology used and discarded would have been very helpful (e.g. agamogony, apogamety, agamospermy, diploparthenogenesis, etc.).

Misprints and errors are few, e.g. "*Linum catharticum*" and "*Cercis siliquastrum* (Mimosaceae)". More attention could well have been given to the lettering of the figures; had larger and better letters been used, many figures could have been improved by substantial reduction. E.J.H.C.

GALL MIDGES OF ECONOMIC IMPORTANCE: VOLUME V: GALL MIDGES OF TREES. By H. F. Barnes. (Crosby Lockwood and Son, Ltd., London, 1951, pp. 270. Price 15s. net.)

Volume V of this important series of publications entitled "Gall Midges of Trees" provides a welcome addition to the five volumes already published, since it treats of all the gall midges of conifers and broad-leaved trees. As Dr. R. N. Chrystal so correctly points out in his Foreword to the book, the volume appears at an opportune period in the history of our forestry development in Britain; we are on the eve of important changes in our forestry policy, especially in the matter of education and research.

This volume is written to a pattern similar to the previous ones and the different species of gall midges are discussed under their respective host plants. The work is divided into two sections, the first section dealing with the gall midges of coniferous trees, and the second discussing the gall midges of broad-leaved trees.

No less than eighty species of gall midges, a large number of which occur in Europe, are associated with conifers. They infest the buds, fruits, terminal shoots, seeds and the cones, while some even live under the bark. The Pine-needle gall midge, *Thecodiplosis brackyntera* Shwag. a well-known pest of young pines on the Continent, has appeared in young plantations in this country in recent years, and may well be a source of worry to the forester in years to come. The first section will prove of great value to the forester, since all the species associated with forestry are referred to in detail, and adequate references are included for the benefit of the research student.

The greater part of the book relates to the gall midges of broad-leaved trees (section II), and over two hundred species are discussed under their thirty-eight host plants. For example, sixteen species of midges are associated with ash, thirteen species occur on beech in different parts of the world and, of the midges which infest willow, three are regarded as economic in view of the injury caused in Cricket Bat willow nurseries in England and elsewhere.

Very little work has been carried out upon the control of midges of conifers and broad-leaved trees, and it is significant that the measures advocated are the time-honoured ones of hand picking and cutting off and destroying the galls. Thus this work may stimulate some student of the group to study some of the species on conifers, with a view to their control in the nursery beds and plantations.

The work contains no less than four hundred and fifty references. The indexes

are also very complete. One lists the generic, specific and popular names of the midges; there is also a plant index and general index.

The book is very well written and produced in a style that is easy to read; it may be regarded as indispensable to the entomologist and those interested in all aspects of forestry and park lands.

A.M.M.

MUSHROOM GROWING. By R. L. O. Jackson. (English Universities Press Ltd., London, 1950, pp. 103, illus. Price 9s. 6d.)

A book on mushroom growing may fall into either of two extreme categories though usually it occupies a place somewhere between. There is the manual which describes the equipment and buildings and gives instructions on the way to produce crops from them; at the other extreme is the diffuse essay which deals little with the actual working of the farm but discusses the probable influence of each operation on the materials used in terms of physics, chemistry and biology. Both types of book have their advocates.

Mushroom Growing is boldly and correctly described on the title page as "a practical manual". It is mainly for beginners. The author, who has himself received training in the biologic sciences and is also a mushroom grower, has succeeded in producing a book of instructions without entering into the realms of speculation. From his opening chapter on First Principles until the index is reached, it is clearly his object to obtain from his commercial unit the maximum quantity of high quality mushrooms and to see that they reach the shopper's basket in good condition.

The chapters on buildings, site and layout, manuring and composting, and management will be of undoubted value to the beginner.

Fifteen pages are devoted to pests and diseases; in these the reader is instructed in methods of hygiene and the author shows restraint by not introducing new but unproved fungicides and insecticides. He treats Mushroom Flies in some detail and, though (or because) he is an entomologist, he gives other animal pests only brief mention, "leaving the grower to make up his own mind whether or not his animal life is dangerous". In considering DDT and Gammexane he warns that races of flies may eventually be bred which are resistant to low concentrations and to overcome this possibility advocates that they should be applied alternately.

The sections on individual fungus diseases and competitors are short but sufficient for beginners. Attention is correctly drawn to the danger of spreading disease from one holding to another by using the same lorries for carrying spent compost and for delivering fresh manure, but there is optimism in believing that a wash-down between operations is an adequate method of removing infected material.

Of the fifty-three text figures, the most valuable are those showing the layout of buildings and equipment.

H.H.G.

A SYNOPSIS OF THE WORLD LITERATURE ON THE FRUIT TREE RED SPIDER MITE *METATETRANYCHUS ULMI* (C. L. KOCH, 1835) AND ITS PREDATORS. By Joan R. Groves. With a brief Review of the Problem by A. M. Massee. (Commonwealth Institute of Entomology, London, 1951, pp. 180. Price 20s. net.)

In compiling this bibliography, Miss Groves and her colleagues at East Malling have rendered a very valuable service to workers concerned with research on red

spider mites. The fact that no less than 1,039 papers have been noticed and annotated is some measure of the increasingly important status of the Tetranychidae as pests; it is also some indication of the herculean labour which compilation must have involved. The manifest need for such a catalogue is shown by the fact that a large proportion of the papers are from journals and bulletins that are unobtainable except in specialist libraries.

Although the Synopsis is devoted principally to *M. ulmi*, many papers referring to other closely related species of economic importance have also been included. The papers are arranged alphabetically under authors, but those dealing with the subject of red spider predators have been collected in a separate section with 218 titles. For reasons of space the annotation is succinct but at the same time it is usually sufficient to convey the gist of the paper. The notes are arranged under a standard series of headings of which "systematics", "dispersal", "bionomics" and "control" are examples. Together, these cover all aspects of the biology and control of red spider mites which are likely to be of particular interest to the economic entomologist.

In the excellent introductory review by Dr. A. M. Massee, reference is made to these different aspects of the red spider problem and attention is drawn to the key works in the bibliography.

A.D.L.

THE FAMILIES OF DICOTYLEDONS. By Alfred Gundersen. (The Chronica Botanica Co., Waltham, Mass.; Wm. Dawson & Sons, Ltd., London, W.C.2, 1951, pp. 230, illus. Price \$4.75.)

Orderly naming and grouping of the species of flowering plants has been a practical necessity from the days of the 16th century herbalists, when the number of species known was relatively small, until modern times when the number known exceeds 100,000. Many of the workers in this field have been associated with the great plant collections in the Botanic Gardens of the world, from the time of Linnaeus of Uppsala to that of Bentham and Hooker at Kew in the 19th century and of Hutchinsonson there at the present time.

Now comes an interesting contribution from America by Dr. Alfred Gundersen of the Brooklyn Botanic Garden.

In past centuries classification of plants was mostly based on superficial resemblances in a very limited number of characters, with the result that groups not infrequently included obviously unrelated species. Indeed, the system of Linnaeus was highly artificial, being based on the common possession of a single floral character, such as one or two, three or four or five stamens and so on. But even where the systems were not, like that of Linnaeus, arbitrarily artificial, there lay behind their arrangements very little idea of natural relationship. Darwin's ideas of the origin of species and of evolution influenced biological thought only from the latter part of the 19th century. Even Darwin's contemporaries, Bentham and Hooker, were uninfluenced by the theory of evolution in their arrangement of plant families.

During the last half century and more, plant taxonomists have applied themselves to the problem of establishing a "Natural System" of classification based on the flower and designed to express the evolution and relationships of groups, orders and families. Fascination lies in the possibilities of differences of opinion and interpretation inherent in attempts to arrange, according to descent, the survivors of the hazards of evolution. There are many missing or imperfect links.

In England the most important recent contributions have been those of Rendle (1925) and more particularly of Hutchinson (1926 and 1948).

Stimulated in the first instance by the ideas of these two workers, Gundersen now offers his interpretation. He agrees with Hutchinson in regarding Magnolia as the most primitive type of flower, but disregards his separation of the groups into woody and herbaceous plants. The scheme followed by Gundersen is set out as a small "family-tree" on page 55. This diagram could with advantage have been given more prominence (a whole page perhaps) since it is the basis of the arrangement of the orders and families. Ten genera are used to typify the stages of evolution of the flowers of Dicotyledons. Starting from Magnolia, the main branch of the tree goes, by way of Cistus, Thea (Camellia), Malva and Geranium to Jasminum. There are two side branches; one from Magnolia to Rosa and then Rubia with a branchlet to Ulmus, and the second from Cistus to Dianthus. These ten genera give their names to the ten groups in which the families are arranged.

Following the introductory chapters, the greater part of the book is devoted to concise descriptions of the families, many of them illustrated by good original drawings by Maud H. Purdy. The whole is preceded, most usefully, by short chapters by specialists on Fossil Dicotyledons, Wood Anatomy, Carpels and Ovules, Embryology, Cytotaxonomy and Plant Geography, which indicate the kind of evidence of relationship and evolution afforded by these branches of Botany.

The book is relatively small and inexpensive considering the amount of information it presents. C.A.P.

MUSHROOM SCIENCE—I. The Proceedings of the First International Conference on Scientific Aspects of Mushroom Growing. (The International Conference on Mushroom Science. Yaxley, Peterborough, England, 1950. Price 7s. 6d.)

The Conference was held at Peterborough from 3rd-11th May, 1950, and during this time more than thirty papers were read. The proceedings are condensed into a booklet comprising 111 pages (Demy 8vo), since, as the editor explains, the field is so specialized, and the expected demand for copies so limited, the cost of publishing a full account would have been prohibitive. The policy adopted was to publish fully new contributions and to summarize any which have been or will be published. Yet the proceedings form a useful review of those lines of investigation which are in progress or which have recently ended.

The papers, which were either accounts of observations or of experimental work, do not readily arrange themselves into simple groups. Broadly, about seven were concerned with methods of cultivation, ten with composts and composting, three with casing materials and six with pests and diseases.

Divergent views were not uncommonly expressed and this is not surprising if account is taken of the variability of the media and of the environment in which mushrooms are grown. Indeed, readers who are unfamiliar with research on mushroom growing could not wish for a better introduction than that given by Edwards in his paper on *Factors Affecting Comparisons Between Yields*. His objects for making comparison were (1) to find the best compost, soil or other material, (2) to find the most efficient system of growing and (3) to serve as a form of operational research (the scientific use of practical observations). In considering the third object, it was hoped to use differences in yields to assess the effects of such major factors as temperature, humidity, ventilation of beds and buildings, types of

building and shape of beds; the method is particularly applicable to the study of those factors which are difficult to vary experimentally. In any comparison between yields the observer normally tries to pick out the most conspicuous differences in conditions and assumes that the others are unimportant; Edwards rightly gives the warning that this assumption is not always justified!

Compost, the very food of mushrooms, was the special sphere of the chemists and their papers reflected much skill and ingenuity of method in dealing with a complex subject. Thus, as a basis for comparison in analytical results, Burrows used acid-insoluble ash as he considered this likely to suffer little alteration in quantity during the composting and cropping period.

Of more immediate interest to the mushroom grower was the contribution by Sinden and Hauser, who gave the advantages of a method of composting in which stable manure could be cured in 7 to 14 days instead of the traditional 20 to 30 days—a method which has found favour in the U.S.A. Practitioners who have long worshipped pH as a guide to composting must have had their faith shaken when Pizer revealed that the reaction of the manure can fluctuate significantly according to its moisture content. Edwards summarized the results of his work on synthetic compost and constructed a useful table on the comparative NPK contents of six formulations which had achieved variable success in recent years. He also showed how the inclusion of several trace elements could increase crop yield.

The casing of mushroom beds had evidently not received much attention since Pizer's pioneering researches at Wye College had shown that soils differed greatly in their ability to stimulate sporophore production. Bels-Koning had not confined her attention to soil alone but also gave the results of observations on casing materials which included marl, Swiss tuff and a mixture of soil and peat. From the data collected she had drawn conclusions on the effects of water-holding capacity, permeability to air, hydrogen ion concentration, nutritive content and water gradient between the casing and the air. Most workers who are familiar with the complexity of the casing problem will agree that these conclusions should be regarded as tentative.

An outstanding feature of recent pronouncements on pests and diseases of mushrooms has been the dearth of experimental evidence of damage done by suspected organisms and of the efficacy of particular therapeutants in their control. The point was emphasized by Hey who detailed some of the newer insecticides now in use and others which might be expected to be useful; he also remarked on the non-employment of recently developed fungicides. This breach was partly filled by the experiments of Yoder, Sinden and Hauser who had found zinc ethylene bis-dithio-carbamate to be successful in the control of the diseases caused by *Mycogone perniciosa*, *Verticillium* spp. and *Dactylium* spp.

Symptoms of two disorders of mushrooms recently observed in the U.S.A. were described by Sinden and Hauser. No organism had been found in association with the one (La France disease) but two moulds, *Spicaria* sp. and *Sepdonium* sp. had been found in the beds where the other (Vern Astley disease) had occurred.

In his concluding remarks, Mr. F. C. Atkins, the Chairman of the Conference, said that interesting and provocative as many of the papers were, he could not help feeling that the greatest value of the Conference had been in personal contacts made and the range and depth of the private talks. Is this not true of all conferences?

H.H.G.

THE ROCK GARDEN AND ALPINE PLANTS. By G. A. R. Phillips. (Collingridge, London, 1951, 2nd ed., pp. 309, illus. Price 15s.)

As a guide to rock garden construction and planting, this book, now in its second edition, is well able to hold its own with a somewhat numerous band of competitors, for rock gardeners are prone to plunge into print with very little provocation. The first part of the book is devoted to construction. The author believes that for full satisfaction the owner should do most of the work himself, or, if this is too heavy, at least be the controlling mind. No set designs, therefore, are provided beyond a few suggestions for treating unusual sites. It is better to await the arrival of the stones before any detailed planning is considered, for their very nature will provide such an infinite variety of possibilities that the conception of the scheme is best left to the man on the spot. However, the methods and principles of construction to be employed are given meticulous attention and, unnecessary as some of them may seem to the exhausted labourer, he can be assured that the author knows his job, prefers plants to stones and never advises two rocks where one will do.

Part II takes the form of a useful guide to the innumerable small perennial plants that it is possible to grow. The more important families, Saxifragas, Primulas and the like, are treated separately. The others are grouped in chapters according to season of flowering. The point of this arrangement is not very obvious since it makes quick reference less easy, and plants in the rock garden are not usually grouped according to flowering date but placed where they are likely to do best. However it is a small point and there is always the index, which happens to be a good one.

Part III consists of chapters on annuals, bulbs, shrubs, ferns and orchids.

Part IV deals with the alpine house, frames and propagation. Both are provided with extensive lists of suitable subjects, with notes on colour, habit and cultural needs. No less than 60 orchids are listed, 200 bulbs, a similar number of alpine house plants and about 160 shrubs. The author can scarcely be accused of not having tried. The book is well illustrated. It can confidently be recommended both to the inexperienced and the expert.

G.St.C.F.

ALPINE HOUSE CULTURE FOR AMATEURS. By G. Anley. (Country Life, London, 1951, 2nd ed., pp. 167, illus. Price 15s.)

The possession of an alpine house is not a *sine qua non* in the successful cultivation of the somewhat exacting beauties dealt with in this book. Indeed, Mrs. Anley, who does not love red tape, seems to think that under present day restrictions, if the house is not already there, it never will be. In any case, its main purpose is to act as a convenient show room. The real work is done off stage in airy frames and shelters which require no licence to erect and are easy on the purse besides. Here the plants in their pots are plunged in sand or ashes and given the maximum of air compatible with protection from unfavourable weather. Better still, they may be grown direct in a compost suited to their needs and make the frame their permanent home. This need not mean a multiplicity of mixtures with a special prescription for each plant, though it is common knowledge that many amateurs regard the concocting of such compounds as a major pleasure. It has been found, however, that in these scree frames the most fastidious plants will flourish in a half and half mixture of chopped fibrous loam and crushed tiles or bricks screened to pea size, provided that there is adequate drainage below. For those who may regard

this as an over simplification, a short series of alternative composts is given, more particularly for plants to be grown in pots. This part of the book contains much sound advice and many useful tips born of the author's long experience. To see her faultless exhibits of "impossible" plants at the alpine flower shows is to realize that her methods will well repay study.

The second part of the book deals with the plants themselves. It consists mainly of long, classified lists of plants suitable for the alpine house, notes on colour and time of flowering, interspersed with occasional, too occasional, comments by the author. Shorter lists and more frequent comment would have increased the interest and added to our knowledge, for while the names of plants and their descriptions can be found in catalogues, their little weaknesses are apt to remain *sub rosa* and a few more revelations would have been welcome. There is much experienced advice on collecting, with special reference to travel. The author will endure discomfort, but not unnecessary discomfort, and a study of this chapter should do much to ease the path of the innocent collector abroad for the first time.

The illustrations, chiefly of pans of rare species sheeted in bloom, are well calculated to arouse both envy and emulation. G.St.C.F.

EARLY POTATOES. By W. L. Thomas and P. W. Eyre. (Faber & Faber Ltd., London, 1951, pp. 198. Price 18s.)

This book describes the methods used by Mr. Thomas for growing early potatoes on his farm in Pembrokeshire. Intended for farmers and market gardeners, the book is written mainly from a practical standpoint and contains chapters on the soil and its preparation, the seed and its treatment, ridging, manuring, planting, inter-row cultivation, lifting and marketing and rotation.

Considerable stress is laid on the need to avoid over-cultivation in the spring, but the authors dismiss the practice of ploughing-in the seed (prevalent in Australia and Tasmania) as not a satisfactory method. It would seem to be worthy of more sympathetic consideration.

Some experiments on the influences on yield of seed size and spacing, number of sprouts per seed, depth of planting and date of first emergence are described, but the data are unconvincing owing to shortcomings in the methods of sampling and lack of experimental designs; the authors themselves draw attention to the inconsistency in yield of individual plants of Arran Pilot, the experimental material. When discussing varieties, they show little knowledge of the principles of genetics and over simplify the potentialities of clonal selection.

Many statements occur that are without scientific justification; for example, "shallow planting gives better potatoes due to less pressure caused by the smaller amount of soil on the tuber"; or, again, "potatoes which flag in the day and assume a turgid, erect position during the night crop earlier, owing to the impulses." This tendency to confuse fact and hypothesis is misleading to the untutored reader.

On the whole, the book is written concisely and clearly and, from the practical aspect, the grower of early potatoes should find much to assist him. K.S.D.

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SYMPTOMS OF MINERAL DEFICIENCY IN CACAO

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IN an account of the cacao industry of the Dominican Republic, Ciferri (1930) described a disease of cacao (*Theobroma cacao* L.) which led to the production of mottled leaves, often abnormally long and narrow or highly curved. He suspected that the affection was due to a virus and at a later date (1948), when he had discovered the same disease in Colombia, he proposed that it should be named "narrow dented leaf virus".

A similar leaf affection was frequently found during the search for swollen-shoot virus in the Gold Coast, Nigeria, and the Ivory Coast from 1940 onwards; it was named "sickle-leaf" on account of its most characteristic deformity. It was at times confused with virus disease, though Posnette (1943) had pointed out that the mottle was one of intervenal chlorosis, as distinct from the vein clearing and banding of virus mosaic; that it was soil-induced and not graft-transmissible.

Sickle-leaf was found to be invariably associated with soils with a high pH value and a high content of available phosphate and potassium; it was particularly prevalent in trees receiving seepage from mounds of rotting cacao husks. Typical symptoms could be induced in healthy plants by digging pieces of rotting husk into the soil or by adding small quantities of the ash of either husk or bean; the addition of 1 gm. potassium carbonate per Kg. soil was also found to induce persistent symptoms (Greenwood, 1943; Greenwood and Hayfron, 1951).

Although symptoms were suggestive of nutrient deficiency, diagnostic tests made in 1944 failed to establish its nature. At that time symptoms of nitrogen, phosphate and potassium deficiencies in cacao had been described by MacDonald (1935) and Hardy (1937), but no account of micronutrient deficiency could be found. The definition of leaf symptoms arising from nutrient deficiency was therefore attempted by the use of water-cultures. The objects were (i) to find the cause of sickle-leaf, (ii) to determine whether, in view of the early confusion of sickle-leaf and virus mosaic, mineral deficiency might be contributory to the many leaf-symptoms later found in association with different strains of virus (Posnette, 1947).

The present paper describes experiments, made in 1945 and 1946, in which cacao seedlings grown in washed sand and distilled water were transferred to nutrient solutions after the cotyledons had been shed. Cacao proved very sensitive to the lack of all the elements tested: without elaborate purification of the reagents employed it was possible, not only to produce typical symptoms of sickle-leaf in various combinations lacking zinc, but also to obtain well-defined symptoms of iron, manganese, boron and calcium deficiencies. Some interesting changes in leaf outline were obtained in cultures lacking both iron and manganese; similar changes were later reproduced by raising the pH of a complete nutrient solution.

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METHOD.

Nutrient solutions.

Since symptoms of sickle-leaf had appeared to be exaggerated by a high concentration of potassium in the soil, it was intended to use both a high and a low K/Ca ratio throughout these experiments. In the first series, solutions of high (K = 250 p.p.m.) and low (K = 50 p.p.m.) potassium levels relative to a fixed calcium level (Ca = 156 p.p.m.) were used. It was unfortunately impossible to continue the use of differential K/Ca ratios in subsequent experiments, in which only the lower potassium level was used.

The solutions used by Reeve and Shive (1944) in studying the effect of the K/Ca ratio on boron deficiency in tomatoes were adopted without modification. Molar concentrations were as follows :

	(i) K = 50 p.p.m.	(ii) K = 250 p.p.m.
Ca(NO ₃) ₂	0.00382 M	0.00252 M
CaCl ₂	0.00008 M	0.00138 M
MgSO ₄	0.00225 M	0.00225 M
KH ₂ PO ₄	0.00112 M	0.00112 M
KNO ₃	0.00016 M	0.00265 M
K ₂ SO ₄	—	0.00132 M

In the complete nutrient solution, trace elements were added in the following amounts : Fe = 1.0 p.p.m. ; B = 0.5 p.p.m. ; Zn = 0.5 p.p.m. ; Mn = 0.25 p.p.m.

"Analar" reagents were used, salts of calcium and magnesium being prepared from their carbonates and the appropriate acids. Distilled water was obtained by the slow distillation of rain-water from a tinned copper still ; it was not further purified. Solutions were first standardized and afterwards adjusted weekly to pH 6.0 by the addition of N/100 H₂SO₄ or N/100 NaOH ; they were daily aerated and brought to constant level by the addition of distilled water. A complete change of solution was made every four weeks.

Seedlings.

Seed of Amelonado type was sown in coarse sand, previously well washed with concentrated HCl ; it was watered with distilled water until the cotyledons had been shed. On transference to culture, seedlings were selected so that the mean height was roughly the same for all treatments ; four replicates of each treatment were used. Single plants were grown in blackened glass jars of 800 ml. capacity ; they were randomized within four groups containing one replicate of each treatment.

Treatments.

Three series of experiments were made, each including complete nutrient (control) and a varying number of other treatments.

Series I. (1) *Complete*, (2) *Minus Iron*, (3) *Minus Boron*, (4) *Minus Manganese*. High and low K levels. Period in sand 60 days ; removed to culture 10 days after shedding cotyledons and completing first flush. (See Table I for dates of sowing and removal to culture.)

Series II. (1) *Complete*, (2) *Minus Magnesium*, (3) *Minus Calcium*, (4) *Minus Iron and Manganese*, (5) *Minus Zinc*, (6) *Iron at concentrations of* (a) 0.5, (b) 0.2, (c) 0.1 p.p.m. Low K level except in treatments 1 and 2 in which Mg and Ca were respectively replaced by their K equivalents, giving (1) K = 224 p.p.m., (2) K = 342 p.p.m. Period in sand 81 days; removed 12 days after completing second flush.

Series III. (1) *Complete*, (2) *Minus Zinc*, (3) *Minus Zinc and Iron*, (4) *Minus Zinc and Manganese*, (5) *Complete Nutrient at* (a) pH 6.2, (b) pH 6.4, (c) pH 6.6, (d) pH 6.8. Low K level. Period in sand: 74 days for controls and treatments 1-4: removed two days after completing second flush; 88 days for treatment 5: these seedlings were still flushing when the other treatments were started; they were irregular in height and only three suitable replicates could be found. Pre-culture heights for all treatments (Table I) were measured at 88 days.

Growth-rate.

Heights were measured at monthly intervals in Series I and weekly in later series; weights were determined when solutions were renewed and when plants were finally removed from culture. Final heights and weights are given in Table I as mean values for each treatment. Where a difference between means has promised interest, significance has been assessed by the "t" test: significance is claimed only when $P < 0.01$.

Flushing.

Leaf-symptoms, summarized in Table II, have been referred to the "flush" of leaf-growth in which they appeared, numbering from the first flush formed in culture.

Cacao is discontinuous in its growth; the leaf-buds of plants of similar age open (flush) at the same time and, after a period of active growth, then enter a period of dormancy from which they emerge together. Mature trees normally produce five flushes per annum under Gold Coast conditions, but in young seedlings the interval between flushes is from four to five weeks (Greenwood and Posnette, 1950). This period was observed with great regularity during the present experiment; within each series plants of different treatments were roughly in phase unless defoliation occurred.

The number of leaves produced in one flush varied from 2 to 7, but was commonly 4; individual leaves of a flush open and mature within a few days of each other. This habit of cacao makes it an easy subject for studies such as leaf injections, since a group of seedlings can be relied on to produce a large number of leaves of similar age. In culture-work it has the disadvantage that, where the onset of symptoms is rapid (e.g. iron, magnesium), observations may be limited to a single flush, though there is often a marked gradation of symptoms within one flush.

DEFICIENCY SYMPTOMS.

Complete nutrient.

Controls in all three series of experiments made good growth similar to that of seedlings planted in good soil. The periods spent in culture ranged from 30 weeks (Series I) to 44 weeks (Series II). Flushes appeared at intervals of about one month;

TABLE I.
Mean heights and weights of plants when removed from culture.

	Treatment.	K p.p.m.	Date finally weighed.	Active culture growth (weeks).	Number of flushes.	Height (mm.).		Final wet weight (gm.).				
						Pre- culture.	Final.	Incre- ment.	Root.	Stem.	Leaves.	Total.
SERIES I. Sown 17.4.45. Culture started 16.6.45.												
1	Complete	50 250	12.1.46	30 30	5 5	100 97	656 650	556 553	17.6 15.8	34.3 40.0	25.9 25.9	77.8 81.7
4	-Mn	50 250	12.1.46	30 30	6+ 6+	98 101	536 483	438 382	13.9 14.6	21.0 22.5	17.3 11.4	52.2 48.5
3	-B	50 250	12.11.45	11 11	2- 2-	102 101	261 268	159 167	2.32 1.85	14.5 14.2	3.84 4.92	20.7 21.0
2	-Fe	50 250	12.11.45	7 7	1 1	99 102	260 266	161 164	1.75 1.60	7.32 6.40	3.55 5.68	12.6 13.7
SERIES II. Sown 7.7.45. Culture started 26.9.45.												
1	Complete	50	30.7.46	44	8	144	723	579	31.8	54.8	43.6	130.2
5	-Zn	50	30.7.46	44	8	141	765	624	34.5	59.9	37.9	132.3
4	-FeMn	50	30.4.46	19	3	135	400	265	7.38	12.8	9.60	29.8
3	-Ca	342	20.2.46	14	2+	136	281	145	2.71	8.88	4.89	16.5
2	-Mg	224	20.2.46	11	2	139	260	131	2.23	7.48	3.61	13.3
6 (a)	Fe 0.5 p.p.m.	50	—	12*	4	135	518	383	—	—	—	—
6 (b)	0.2 "	50	—	12	3	137	301	164	—	—	—	—
6 (c)	0.1 "	50	—	12	3	142	295	153	—	—	—	—
SERIES III. Sown 14.1.46. Culture started 30.3.46 (1-4) ; 14.4.46 (5).												
1	Complete	50	11.11.46	32	7	181	610	429	26.7	38.1	45.2	110.0
2	-Zn	50	11.11.46	32	6	181	570	399	26.2	39.4	39.6	105.2
4	-MnZn	50	11.11.46	32	7	165	499	334	25.0	32.8	37.9	95.7
3	-FeZn	50	11.11.46	32	5+	179	439	260	22.4	30.5	20.0	72.9
5 (a)	pH 6.2	50	11.11.46	30	4+	162	442	280	16.3	20.8	26.9	64.0
5 (b)	pH 6.4	50	11.11.46	30	5-	165	417	252	13.4	17.2	21.0	51.6
5 (c)	pH 6.6	50	11.11.46	?	2+	170	296	126	8.7	11.7	8.3	28.7
5 (d)	pH 6.8	50	11.11.46	?	2-	177	302	135	8.5	11.7	3.7	23.9

Flushes + —. Individual plants producing more or fewer than the mean number of flushes.
Growth Period *. Removed from culture whilst active.

TABLE II.

Summary of Leaf Symptoms.

Deficiency.	Symptoms (Numbers denote flushes).
1. <i>Iron</i>	(1) Sharply defined vein pattern of darker green against whitish green background: tip scorch followed by marginal scorch and ultimate leaf-shedding. Aggravated by low potassium level, forming ivory-white crinkled leaves with downward tip curl, rapidly shed after tip, marginal and interveinal scorch. Petioles erect: main stem and petioles mottled purplish-brown.
2. <i>Boron</i>	(1) Angular flecks of pink pigment becoming first transparent then rusty as leaf ages. (2) Thick leathery leaves with inverted-boat curvature: thickening at base of main stem and mid-rib: reddish stripe along mid-rib: death of terminal bud and production of axillary shoots bearing small curved leaves.
3. <i>Manganese</i>	(1, 2) Normal. (3) Diffuse dark green vein shading, against yellow green background: pin-pointing of yellow spots. (4) Yellow strips between laterals and around margin. (5) Transparent strips pin-pointed reddish-brown parallel to mid-rib, turning deep yellow on ageing: marginal scorch with inward roll: leaf shedding, accelerated by high potassium level.
4. <i>Magnesium</i>	Indeterminate: general chlorosis and shedding of all leaves.
5. <i>Calcium</i>	(1) Uniform pale green chlorosis: large whitish spots alongside mid-rib: mid-rib thickened at base, edged in purple. (2) Uniform chlorosis: rapid shedding of all leaves.
6. <i>Iron and Manganese</i> ..	(1) Mild iron chlorosis. (2) Severe iron chlorosis and rapid leaf-shedding. (3) Dentate leaves: sharp-cut vein-pattern of iron chlorosis: tip scorch on ageing.
7. <i>Zinc</i>	(1, 2) Normal shape: bluish tinge: corrugation: characteristic primrose mottle on ageing. (3-8) Raised distorted vein-pattern: lateral curvature or long narrow leaves (sickle-leaf): little or no leaf shedding. Vein-clearance in flaccid and chlorotic tip shown by three plants in (4, 5) of Series II: not reproduced in Series III.
8. <i>Zinc and Iron</i>	(1-3) Mild iron chlorosis, only one leaf with acute symptoms: raised vein-pattern and curvature of sickle-leaf. (4-6) Curved and elongated whitish green leaves, developing elliptical necrotic patches between laterals: leaf shedding.
9. <i>Zinc and Manganese</i> ..	(1) Normal. (2) Mottle similar to (1, 2) of -Zn. (3, 4) Vein-shading, deep yellow chlorosis as in (3, 4) of -Mn. (5-7) Lateral curvature and elongation of -Zn.
10. <i>Complete, pH 6.2-6.5</i>	(1) Mild chlorosis: parti-coloration: tip-scorch. (2) Severe iron chlorosis and rapid leaf-shedding. (3, 4) Broad leaves slightly denticulate: acute dentation in leaves of normal proportions: irregular dark and whitish green pigmentation. (4, 5) Gradual passage from previous symptoms to leaves of normal shape with blurred vein-pattern and yellow-green chlorosis of -Mn.
11. <i>Complete, pH 6.6-6.8</i>	(1, 2) Severe iron chlorosis, rapid leaf shedding in second flush. (3) Highly curved white leaves similar to -FeZn: death of terminal bud and development of axillary shoots.

the only notable irregularity occurred in plants of Series II which, during a period of extremely low humidity in January, 1946, failed to produce the expected flush.

In all young leaves there were mild symptoms of iron deficiency. Usually these symptoms disappeared as the leaves aged, but they attained some severity in the seventh flush of Series II which was showing tip scorch when plants were removed from culture. Plants were then over a year old and had begun to shed leaves of the first flush; shedding in controls of other series was confined to pre-culture flushes. Experiments described later suggest that the provision of 1.0 p.p.m. Fe in the basic solution was adequate; they point to faulty pH control as the cause of iron deficiency.

The potassium level (Series I) had no effect on plant height or on total weight. Plants at the higher level were more robust and had significantly heavier stems, but this difference was partly offset by the noticeably greater rootlet development in plants at the lower level; as here measured, by weighing the total root system, this difference was not significant.

Iron (Series I).

All plants produced one flush, coincident with the first control flush, during their third week in culture. They had ceased elongation by the seventh week and there was no further attempt to form either leaves or axillary shoots. Growth from the outset was poor; stems were spindly and root development was negligible.

Chlorosis was apparent in all leaves within ten days of emergence. The early leaves of the flush were pale green, with veins sharply outlined in normal green; succeeding leaves became increasingly chlorotic, the last leaves of the *high* potassium plants being whitish green with light green veins; these leaves were firm and of normal shape.

Chlorosis was much more severe in leaves of the *low* potassium plants, the final leaves of the flush being ivory-white, of crinkled papery texture and hooked downwards at the tip, except for the mid-rib which was a faint yellow-green with colourless veins (Fig. 7). Tip scorch and rusty intervenal spots appeared on the papery leaves when they were six weeks old; the earlier low-potassium leaves began to develop tip scorch about two weeks later. Marginal scorch followed, and shedding began when the leaves were 15 weeks old. The entire flush was shed within the course of a week.

Leaves of the high-potassium plants were 12 weeks old before tip scorch appeared, and only one leaf had been shed at the time that all the low-potassium leaves had fallen. Nine leaves, then 19 weeks old, were still retained when plants were removed from culture.

All plants were distinguished by the erection of the petioles which made an angle of 5° with the stem, compared with an angle of 50° made by the controls, and by the presence of a purple-brown mottle which covered all parts of stems and petioles developed in culture.

Boron (Series I).

Two flushes, synchronous with the control flushes, were formed. Growth was poor; plants were stunted and, despite their longer growing period, their final height was no greater than that of plants lacking iron. They were, however, significantly

heavier, particularly in respect of stem weight. Stems of all plants were thickened at the base and had a marked taper (Fig. 5). Rootlet growth was poor but noticeably better than in plants lacking iron.

In the first flush, three plants (all high-potassium) produced normal leaves; there were striking symptoms in the later leaves of the other five plants. Young cacao leaves are pink and pass through bronze to green whilst maturing. In the affected leaves angular flecks of pink pigment remained during the bronzing stage, becoming transparent as the leaf turned green (Fig. 6), finally turning rusty as the leaf aged. Leaves of this flush were retained throughout the plants' life except in one plant (low-potassium) which shed all its leaves when they were 12 days old.

Six plants formed a second flush. All leaves were distorted on emergence; when mature they were sage-green, leathery, and had inverted-boat curvature. The last-formed leaves were small; they developed warm russet tips and marginal scorch, and patches of intervenal scorch when about three weeks old; they began to shed three weeks later. The mid-ribs of the earlier leaves of the flush were then showing marked thickening near the petiole, some appearing as though they were about to split. Thickening was in many cases preceded by the appearance of a reddish-purple stripe on each side of the mid-rib. When about 8 weeks old, a number of these leaves developed small discrete whitish-green patches which later became scorched; many had been shed when plants were removed from culture.

The terminal bud of the plant which shed its first flush was dead when, four weeks later, the plant began to produce shoots from secondary nodes. These shoots formed a succession of leathery distorted leaves, similar to those of the main second flush. There was a gradual decrease in leaf size and the final leaves began to shrivel and drop when about 2 cm. long (Fig. 5).

The potassium level had no noticeable effect on growth.

Manganese (Series I).

All plants survived as long as the controls. They formed five flushes coincident with the control flushes, an extra flush, between the fourth and fifth control flushes, appearing after defoliation of the fourth flush had begun. A number of flushes of small leaves, rapidly shed, were formed shortly before plants were removed from culture.

Though the initial growth-rate was good, plants were significantly shorter than the controls at the start of the third flush; they were significantly lighter at the time of the fourth flush and the difference was rapidly widened by the defoliation which followed this flush (Fig. 1). Plants had unexpectedly well-developed roots (Fig. 1) and the final total root weight was not significantly less than that of the controls.

All plants in their first two flushes and four plants in their third flush produced normal leaves. Chlorosis was first observed in the last-formed leaf of four plants (two high-, two low-potassium) in their third flush: it was present in all leaves of the fourth flush. In contrast to the clear-cut vein pattern of iron chlorosis, veins were diffusely shaded by dark green pigment which gave them a blurred appearance. The leaf background was yellow-green as opposed to the whitish-green of iron deficiency. Numerous transparent pin-points that turned yellow as the leaves aged, were present in the intervenal spaces of young leaves. Parallel strips of lemon-yellow then appeared between the lateral veins, gradually spreading to the margins where

they united to form a continuous rim round the leaf. Marginal scorch followed, and the youngest leaves began to shed when about three weeks old.

In the fifth flush, leaves were pale yellow-green with shaded dark green veins. When young, many had transparent strips, pin-pointed with reddish-brown, running parallel to the mid-rib; the strips turned deep canary-yellow as the leaves matured. All leaves of this flush were shed about 20 days after emergence. Similar symptoms were produced in the sixth flush in which leaves were smaller and puckered. Scorch quickly appeared in the margins, causing the leaves to fold inwards; they were shed when 14 days old. Flushes of very small leaves, rapidly shed, appeared on six plants at irregular intervals during the following month.

The potassium level had no effect on early growth but, from the fourth flush onwards, the low-potassium plants began to gain in height. The increments gained between this time and the end of the experiment (25.9.45 to 12.1.46) were significantly different: K50 = 144 mm.: K250 = 99 mm. Leaf-shedding was noticeably less rapid in the low-potassium plants which retained a significantly higher weight of leaves at the final weighing (Table I). This evidence that a low potassium concentration, found to exaggerate iron deficiency, may reduce the severity of manganese deficiency, appears to be in agreement with observations on other orchard crops, e.g. citrus (Chapman, Brown and Rayner, 1945).

Magnesium (Series II).

Plants formed only two flushes. Growth was very poor; stems were spindly and there was very little rootlet development.

Leaves of the first flush were normal in shape, uniformly yellow-green with light green veins. They gradually turned yellow; margins and tips developed scorch when about 7 weeks old and shedding began soon afterwards.

In the second flush, leaves were small, whitish-green or translucent and had a marked downward tip-curl; all were shed within 20 days of emergence. Considerable shedding of pre-culture leaves had occurred when plants were finally weighed (Fig. 2).

Calcium (Series II).

Two main flushes were formed. Growth was of the same order as that in plants lacking magnesium; stems were slightly thicker and rootlets more numerous (Fig. 2).

Leaves of the first flush were of normal size and shape and were only faintly chlorotic. When these leaves were 8 weeks old, pin-points developing into whitish spots, about 3 mm. in diameter, appeared alongside the mid-ribs which later became swollen towards the base; in the leaves of two plants the thickened veins were edged in purple. Leaves began to shed when 14 weeks old, after having developed progressive tip scorch, scorching near the mid-rib and occasional marginal scorch.

The second flush consisted of small leaves, of a uniform pale green, that rapidly developed interveinal and tip scorch and were shed when 4 weeks old. Two plants then attempted abortive flushes of small leaves that were shed within a week of appearance. As with plants lacking magnesium, defoliation had occurred in pre-culture flushes when plants were removed from culture.

The similarity of some of these symptoms to those observed in plants lacking boron will be noticed.

Iron and Manganese (Series II).

All plants formed two flushes coincident with the first two control flushes. A third flush, anticipating the third control flush, began soon after the shedding of the second.

The dominant feature of the first flush was mild iron chlorosis: leaves were pale green, with a vein pattern clear-cut in normal green. Progressive tip scorch began to appear when they were about 4 months old and shedding began a month later.

There was acute iron chlorosis in the second flush. Early leaves were whitish green, while the last were cream and had the papery texture and inverted-boat curvature of the low potassium plants lacking iron in Series I. All leaves were shed within three weeks of emergence, after developing tip, marginal and intervenal scorch.

There was only mild chlorosis in the third flush. There was a gradation from pale green in the early leaves to yellow-green in the later ones; the vein pattern was sharp. There were 15 leaves in the flush and, of these, 11 were sharply dentate. In the more mildly affected leaves, dentation was confined to the tip (Fig. 8); in others it occurred along the whole periphery. Tip scorch appeared in some of the earlier leaves when they were about 16 weeks old, and had progressed about 2 cm. when, two weeks later, plants were removed from culture to obtain unscorched leaves for analysis.

Iron at reduced concentration (Series II).

The appearance of iron chlorosis in the controls suggested inadequate provision of iron in the complete nutrient solution. Since no apparent benefit resulted from increasing the iron concentration from 1.0 to 2.0 p.p.m., solutions containing (a) 0.5, (b) 0.2 and (c) 0.1 p.p.m. Fe were tested in order to determine how low an iron concentration the plants would tolerate.

The experiment was discontinued after 24 weeks, when all plants at the two lower Fe levels had died after producing one flush showing mild to acute chlorosis, and two flushes of small, cream, papery leaves which were rapidly shed.

Plants receiving 0.5 p.p.m. Fe formed four flushes at the same time as the controls, the leaves showing only the faint signs of chlorosis present in the controls. There was no difference in the growth-rate of the two sets of plants, the heights at 24 weeks being, with 1.0 p.p.m. Fe, 528 mm. and, with 0.5 p.p.m. Fe, 518 mm. Thus, a concentration of 1.0 p.p.m. Fe in the complete nutrient should be adequate for growth.

Zinc (Series II and III).

In both series of experiments growth was good, the plants being at no time less in height or weight than the controls. There was some irregularity in growth and, in Series III, plants produced one flush fewer than the controls. This irregularity and the lack of any ordered progression of symptoms point to the introduction of a fluctuating supply of zinc, either in the reagents or in the water which was obtained by distillation from rain-water collected from a galvanized iron roof.

Mottling, readily recognizable as the first symptom of sickle-leaf disease, occurred in the first and second flushes of all plants of Series II and in the second flush of Series III. Young leaves were normal in size and shape, but were bluish-green and lacked lustre. On ageing, the intervenal spaces arched into folds convex

to the upper leaf surface, giving the leaf a corrugated appearance. Pale yellow, raised patches began to form on the crest of the arches when leaves were 4 weeks old, their number gradually increasing until many leaves were covered by a dark-green and primrose mottle (Fig. 3).

There was leaf curvature and a distorted raised vein pattern in the second flush of one plant of Series II and in the third flush of one plant of Series III. The other leaves of the third flush were apparently normal, and curvature became common only in the fourth flush in which leaves were mildly chlorotic on first appearance. The vein pattern was distorted. Veins were raised above the surface, becoming dark green as the leaf aged, whilst the light green pits between the veinlets gradually turned yellow. There were good examples of highly curved leaves (Fig. 4) and of straight elongated leaves, waisted near the petiole and with a drawn-out tip, sometimes slightly incised (Ciferri's "narrow dented leaf") in this and all subsequent flushes, though there were a number of apparently normal leaves in every flush. There was little tip scorch and leaves were retained throughout the experiment.

In Series II, three plants in their fourth flush produced a total of seven leaves in which the tips were light green and flaccid, transparent near the veinlets. Similar vein-clearance and flaccidity occurred in the tips of one leaf of each of two plants in the fifth flush. This symptom was not reproduced in Series III.

Zinc and Iron (Series III).

All plants formed four flushes coincident with those of the controls; two plants formed a fifth and there was an abortive sixth flush on the part of three plants. Their final weights were significantly less than those of plants lacking only zinc, and they were shorter after 4 months in culture.

Leaves of the first flush were whitish-green and corrugated when young; on ageing they developed the raised and shaded vein formation of sickle-leaf. One leaf had pronounced lateral curvature and one had inverted-boat curvature and rapidly developed tip scorch.

The second flush was normal except for corrugation and slight chlorosis, but all leaves of the third flush were chlorotic with distortion similar to that of the first flush; one leaf on each of two plants had lateral curvature.

In the fourth flush, all plants produced sickle-leaves of a much paler colour than those formed by plants lacking only zinc. Of 17 leaves, only 4 were of normal shape, 11 were highly curved and 2 were long and narrow. On ageing, the tips became scorched and elliptical necrotic patches appeared between the laterals. This symptom also appears in seedlings grown in soils given a liberal application of cacao bean ash. Leaves of the fifth flush were normal in shape but all leaves of the sixth flush were highly curved and narrow and were shed within 14 days of emergence.

There was no treatment lacking iron only in this series, but there is no reason to suspect that the $-\text{FeZn}$ solutions contained more iron than the $-\text{Fe}$ solutions of Series I or the 0.2 p.p.m. Fe solutions of Series II. It is noteworthy, therefore, that only one leaf (Flush 1) of this treatment showed symptoms of acute iron chlorosis and that the life of the plants was much longer than that of those lacking iron but supplied with zinc. This behaviour supports the observation of Hewitt (1948) that between iron and zinc there is a relationship parallel to that between iron and manganese (Somers and Shive, 1942), i.e. that a reduction in the zinc level may mitigate the symptoms of iron deficiency.

Zinc and Manganese (Series III).

Plants made good growth and flushed with great regularity. They were shorter than plants lacking only zinc; their final weight was less, but not significantly so.

Leaves of the first two flushes were normal in shape and colour when young; the mottle of zinc deficiency appeared in the second flush after 12 weeks.

Symptoms of manganese deficiency of increasing severity occurred in the third and fourth flushes, in which all leaves were of normal shape. Vein-shading against a yellow-green background was followed by yellowing between the laterals; tip and marginal scorch developed as the leaves aged. A number of sickle-leaves appeared in the fifth, sixth and seventh flushes.

Complete nutrient at high pH (Series III).

Since tip dentation similar to that observed in the —FeMn plants (Series II) had been noticed in seedlings growing in calcareous soil, it seemed likely that some interesting effects might be obtained by raising the pH of a complete nutrient solution. Plants (three replicates only) were therefore grown in solutions adjusted weekly to pH, (a) 6.2, (b) 6.4, (c) 6.6, (d) 6.8. In the controls there was normally a rise from pH 6.0 to pH 6.2 during a week. Weekly pH ranges at the higher levels were: (a) 6.2–6.4, (b) 6.4–6.5, (c) 6.6 stable, (d) 6.8–6.7.

There was no significant difference between the growth-rates of treatments (a) and (b), which produced plants roughly half the weight of the controls, or of (c) and (d) which in turn produced plants only half the weight of those of (a) and (b). The striking difference in growth between the controls and plants adjusted to pH 6.2 makes it very apparent that it would have been advisable to use a lower or more rigidly standardized pH throughout these experiments; it also seems likely that the symptoms of iron deficiency noticed in the controls were caused by too high a pH.

pH 6.2–6.5. Leaves of the first flush were whitish-green when young, with a gradual accession of pigment as they aged. In five leaves the spread of pigment was arrested, leaving a parti-coloured leaf of a type frequently noticed in plants growing in calcareous soil. There was a progressive decrease in pigmentation passing from the petiole to the tip of one lamina and returning via the tip of the opposite lamina to the petiole. Tip scorch appeared in all leaves when they were about 8 weeks old.

All plants next formed a flush of white papery leaves that were shed within 20 days of emergence. After an unusually long resting period, varying from 7 to 15 weeks, they then produced flushes which all contained leaves of abnormal shape. Some of the early leaves were of normal outline; they were followed by leaves which were abnormally broad (ratio of length/breadth = 4/3, compared with 3/1 for a normal leaf) and only slightly crenate, or by sharply denticulate leaves of normal proportions. Succeeding leaves became increasingly dentate. All leaves showed symptoms of mild iron chlorosis. The vein pattern was sharp, the background changing from whitish-green to light green as the leaf aged; in one or two leaves there was irregular pigmentation (Fig. 9).

The fourth flush appeared after a normal period of dormancy. In three plants all leaves were of normal shape; in the others the first leaf was acutely dentate (one was trilobate in appearance) and the remainder normal or only slightly wavy. In some leaves there were blotchy pigmentation and faint signs of iron chlorosis;

in others, the leaf was yellow-green with vein shading ; in the last leaves of one plant there were yellow strips between the laterals suggestive of manganese deficiency.

Two of the plants at the higher pH formed a fifth flush in which the leaves were yellow-green with vein shading and of normal shape. They were very slow to develop and the final leaves were still immature when the experiment closed.

pH 6.6—6.8. Leaves of the first flush of five plants were whitish-green with a sharp vein pattern and normal in shape. Tip scorch appeared at 6 weeks and was followed by marginal scorch, shedding beginning at 20 weeks. The sixth plant (pH 6.8) formed three whitish leaves of which the first was normal and the second two sickle-shaped ; it failed to flush again.

Five plants formed a second flush of which the leaves were white and papery and were shed before reaching maturity. Only two plants flushed again. One (pH 6.8) produced four whitish-green leaves of which two were dentate and two sickle-shaped : they rapidly developed tip scorch but were retained to the end of the experiment. The other (pH 6.6) developed a sequence of four monthly flushes consisting of (1) abnormally large leaves, some denticulate and parti-coloured, (2) whitish leaves of normal shape, (3) yellow-green leaves with vein shading, (4) cream leaves with pronounced lateral curvature.

When plants were removed from culture, axillary shoots were appearing on three of the plants which had formed only two flushes.

DISCUSSION.

Despite their apparent content of appreciable amounts of zinc, the $-Zn$ cultures reproduce all the symptoms of sickle-leaf normally encountered in nursery seedlings. The vigour of the plants is consistent with that of seedlings transplanted to a medium containing a high proportion of cacao leaf litter : sickle-leaf may appear in the next flush whilst plants are growing rapidly and producing leaves larger than normal.

Plants in the $-ZnFe$ treatment exhibit the more severe symptoms shown by seedlings potted in soils containing cacao bean ash ; such seedlings show an increasing response to leaf paintings with ferrous sulphate as the severity of the symptoms increases. There is some response to iron by young curved leaves showing only mild symptoms of sickle-leaf, but painting with a mixture of ferrous and zinc sulphates produces a more certain response than zinc sulphate alone (Greenwood and Hayfron, 1951).

It is uncertain whether the tip flaccidity and chlorosis produced in the $-Zn$ plants of Series II are a genuine symptom of zinc deficiency. It is of some interest as the attendant vein-clearance bears a strong resemblance to the vein-clearance and fern pattern of the attenuated form of virus strain A (Posnette, 1947. Pl. 8. Figs. 2 and 6). No other deficiency symptom here described is likely to suffer confusion with symptoms of virus.

The progression of symptoms in seedlings maintained between pH 6.2 and 6.5 is an orderly one for which the work of Somers and Shive (1942) provides a plausible explanation.

There are three phases. The first covers two flushes and is marked by iron deficiency of increasing severity. There is evidence from the $-Mn$ and $-MnZn$ cultures that, during this period, the manganese introduced with the seedling remains

mobile. The acute chlorosis which causes rapid defoliation in the second flush probably arises, therefore, whilst the ratio of available Mn/Fe is very high.

After a long resting period, plants enter a second phase, of very short duration, in which leaves are abnormal in size and shape and exhibit only mild symptoms of iron chlorosis. This phase passes smoothly into a third in which leaves are of normal shape and show symptoms of manganese chlorosis.

There is evidence of a gradual decline in the Mn/Fe ratio during the passage from the first to the third phase, and it seems likely that, at some intermediate stage, both Fe and Mn are reduced to critical amounts similar to those present during the third flush of the —FeMn plants. Why leaf shape should then show such vagaries is a matter for speculation. Skoog (1940) has shown that auxin is readily inactivated in the absence of zinc, which appears essential to a protective oxidation-reduction system. It seems not unlikely that a similar system, demanding the presence of critical amounts of Fe and Mn, may be essential to the stability of the factor which determines normal leaf shape in cacao.

SUMMARY.

1. Leaf symptoms developed by cacao seedlings grown in water-cultures containing limiting amounts of iron, manganese, iron-manganese, boron, magnesium, calcium, zinc, zinc-iron, zinc-manganese are described.

2. The symptoms appearing in all combinations lacking zinc are identical with those of "sickle-leaf" disease of West Africa. The most acute symptoms are shown by plants lacking both zinc and iron, in which growth is noticeably greater than in plants lacking only iron.

3. The dentation observed in the leaves of plants growing in calcareous soil has been reproduced in highly exaggerated form in solutions lacking both iron and manganese and in complete nutrient maintained between pH 6.2 and pH 6.5.

4. An increase in the K/Ca ratio produces heavier stems in plants grown in complete nutrient; it delays the appearance of acute chlorosis in plants lacking iron; it retards growth and accelerates leaf-shedding in plants lacking manganese.

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This paper is published by kind permission of Mr. S. D. Ross, Director of the Gold Coast Department of Agriculture, and Mr. J. West, Director of the West African Cacao Research Institute.

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PLATE I



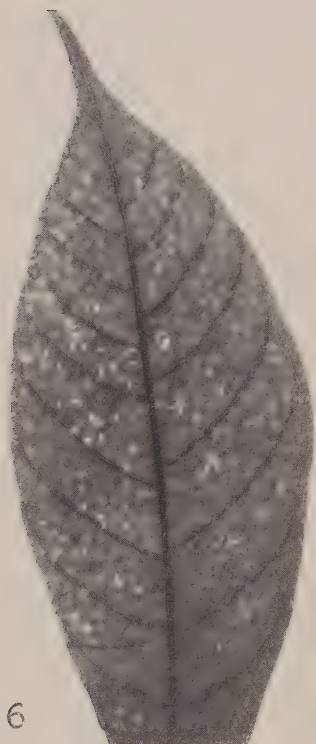
FIG. 1. *Control v. Minus Manganese*. Defoliation in —Mn plant at high potassium level (Series I).

FIG. 2. *Minus Calcium* (left) *v. Control v. Minus Magnesium* (right) (Series II).

FIG. 3. *Minus Zinc*. Leaf mottle in first flush (Series II).

FIG. 4. *Minus Zinc*. Lateral curvature (sickle-leaf) and raised vein pattern in fourth flush (Series II).

FIG. 5. *Minus Boron*. Thickening of main stem and mid-ribs, leaf curvature and axillary shoots bearing small leaves (Series I).



6



7



8



9

FIG. 6. *Minus Boron*. Angular leaf fleck in first flush (Series I).

FIG. 7. *Minus Iron*. Crinkled ivory leaves with inverted-boat curvature and interveinal scorch; last leaves of first flush of plant at low potassium level (Series I).

FIG. 8. *Minus Iron and Manganese*. Dentation confined to tip. Symptoms of mild iron deficiency including tip scorch developed on ageing. Third flush (Series II).

FIG. 9. *Complete Nutrient at pH 6.4*. Acute dentation and irregular pigmentation. Third flush (Series III).

EXPERIMENTS ON THE CONTROL OF BROWN ROT OF APPLES AND PLUMS

III. SUMMER SPRAYING TRIALS*

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THIS paper deals with experiments on the control of brown rot of apples and plums (caused by *Sclerotinia fructigena* Aderh. and Ruhl. and *Sclerotinia laxa* Aderh. and Ruhl.) by means of summer applications of fungicides to the developing crop.

It is generally accepted that the routine orchard fungicidal sprays, such as lime-sulphur and Bordeaux mixture, are of little direct value in controlling brown rot of fruits. Recent developments of organic fungicides of high toxicity led workers, both in this country and in America, to investigate their possible use against these diseases.

In England such trials met with varying success. While Bennett, Kearns and Marsh (1945) obtained fairly promising results, those of Moore (1950a, b) were disappointing. Reviewing the problem of the control of brown rot of apples in the light of his trials, Moore stressed the significance of fruit injury as a factor in infection, and suggested that local conditions might play a large part in the success or failure of summer fungicidal spray applications. He considered that, in general, summer spraying was likely to be effective only when the spray application happened to coincide with a peak period of fruit injury. Such injury is often due to attacks by apple scab and codling moth, and Moore showed that sprays aimed at these wound agencies resulted in a significant indirect control of brown rot.

The following notes briefly describe former experiences with the three fungicides which were tested at Long Ashton in 1950 in the experiments recorded below.

Phenyl mercury chloride. This compound has been tested by Moore (1950a) against apple brown rot. Although it is used to some extent as a routine spray against apple scab (caused by *Venturia inaequalis* (Cooke) Wint.) in this country, one or two applications at the rate of 0.005 per cent. active material were ineffective against brown rot at East Malling.

On the other hand, it showed promise in preliminary trials against brown rot of plum (Byrde, 1949, 1950), and laboratory tests have shown its outstanding toxicity to conidia of *S. fructigena* (Byrde, 1952a).

Dichloronaphthaquinone. 2 : 3-dichloro-1 : 4-naphthaquinone was included by Hamilton (1948, 1950) in tests against brown rot of peach in New York. He considered in 1948 that it might prove to be the most effective of the fungicides which he tested ; it dried up broken tissue and should thus show to advantage after storage and transit of the fruit, while it was more effective than sulphur in his 1949 trials. Foster (1949), however, found it no better than sulphur in trials of spray schedules containing various fungicides. Widespread phytotoxicity has been a serious drawback to its use in America.

* The investigations published in this paper formed part of the work undertaken for the Degree of Doctor of Philosophy of the University of Reading. The 1948-1950 trials were carried out mainly at Long Ashton Research Station, by kind permission of the Director.

In a preliminary trial at Long Ashton against brown rot of plum, a 50 per cent. commercial formulation of dichloronaphthaquinone applied in late June showed promise, though causing fruit spotting (Byrde, 1950). It showed high toxicity *in vitro* to conidia of *S. fructigena* (Byrde, 1952a).

N-trichloromethylthio-tetrahydrophthalimide, a newly developed fungicide, was also tested by Hamilton (1950) against brown rot of peach. Although superior to sulphur, it was less effective than zinc dimethyldithiocarbamate and dichloronaphthaquinone. Preliminary laboratory trials indicated that it is highly toxic to conidia of *S. laxa* (1952a).

EXPERIMENTAL.

MATERIALS USED.

Phenyl mercury chloride, as a mixture with kaolin in the ratio of 39 parts kaolin : 1 part phenyl mercury chloride. This 2.5 per cent. preparation will be referred to as Formulation "C".

2 : 3-Dichloro-1 : 4-naphthaquinone, as a commercial 50 per cent. wettable powder.

N-trichloromethylthio-tetrahydrophthalimide, as a wettable powder containing 50 per cent. active material.

ASSESSMENT OF INFECTION.

During 1948 and 1949, brown rot infection of plums had been recorded by picking a sample of 200 to 250 fruits from each tree, taking them from a convenient cone-shaped section on a predetermined aspect and extending to the centre. Fruit showing any brown rot infection had been classified as infected.

The technique was improved in 1950 by distinguishing between "primary" and "contact" infections, and at the same time recording the number of healthy fruits showing breaks in the skin. By this means, the proportion of wounds which had become infected could be estimated.

A method originally due to Moore (1950c) was slightly modified for the recording of brown rot infection of apples. A labelled branch on each tree was examined weekly from mid-August: infected fruits were picked off and recorded on each occasion. In addition, on the branch, the number of healthy fruits showing skin injury was recorded at picking time, in order to estimate what proportion of total injuries had become infected.

TRIAL ON BROWN ROT OF PLUM.

A further trial on the lines of that carried out in 1949 was undertaken in 1950, using the same sixteen Victoria plum trees. Four trees were allotted to each treatment and four trees served as unsprayed Controls.

The fungicides used were as follows:

- | | | |
|--|---------|--------|
| (a) <i>Phenyl mercury chloride</i> (Formulation "C") (equivalent to 0.00375 per cent. pure material) | | 0.15% |
| (b) <i>Dichloronaphthaquinone</i> (50 per cent.) | | 0.075% |
| <i>Epsom salts</i> | | 0.075% |
| (c) <i>N-trichloromethylthio-tetrahydrophthalimide</i> (50 per cent.) | | 0.2% |

Before the sprays were applied, two mummified apples bearing sporing pustules of *S. fructigena* were hung on opposite sides of each of the sixteen plum trees, to act as a fairly uniform source of infection. No other mummified fruits were present on the trees.

The fungicides were applied on 7th July, 1950, by means of a bucket sprayer, at the rate of 3 to 4 gallons per tree. An excess of wetting agent was added to each spray to ensure thorough wetting of the fruits. Weather conditions were favourable and no rain fell during the ensuing 48 hours.

A further spray was applied to six of the trees, using the same materials, on 3rd August, 1950. The plum fruits wetted more easily at this stage and the wetting agent was omitted, except in the phenyl mercury chloride wash where it was added at reduced strength. Weather conditions were again favourable and no rain fell during the ensuing 48 hours.

Fruit infection was recorded on 16th and 18th August, on a sample of 250 fruits from each tree, taking into account the number of healthy fruits showing skin injury and distinguishing between primary and secondary infections. Table I shows the proportion of total damaged fruits which had become infected.

Chi-square analysis of the data of Column (4) shows no treatment to be significantly better than the Control. A consideration of data from sprayed trees only, however, indicates that, in general, two sprays were significantly better than one spray. No statistical analysis was carried out on the data of Column (5); the interpretation of these figures is difficult for such small samples, since the presence or absence of contact infections is governed primarily by the density of the fruit.

TABLE I.

Brown rot infection of Victoria plum on 16th and 18th August, 1950.

(1) Treatment.	(2) No. of applica- tions.	(3) Tree no.	(4) Proportion of damaged fruits infected	(5) Contact infections expressed as proportion of total infections
Control	—	1 2 3 4	0/7 5/13 10/21 7/20 } 22/61	0/0 6/11 4/14 9/16 } 19/41
Phenyl mercury chloride	2 1	5 6 7 8	7/34 5/16 12/19 7/10 } 12/50 19/29	0/7 0/5 21/33 25/32 } 0/12 46/65
Dichloronaphthaquinone	2 1	9 10 11 12	2/14 11/46 6/20 12/27 } 13/60 18/47	10/12 0/11 6/12 26/38 } 10/23 32/50
N-trichloromethylthio-tetrahydrophthalimide	2 1	13 14 15 16	11/23 9/31 3/13 14/27 } 20/54 17/40	3/14 5/14 5/8 19/33 } 8/28 24/41

TRIAL ON BROWN ROT OF APPLE.

In view of the successful results from summer spraying trials on plums in 1948 and 1949, a trial on apples was carried out in 1950. Owing to the long season for possible infection of the fruit, it was clear that more than one spraying would be required and it was decided to use two applications, one in mid-July and one in mid-August.

The experiment was carried out on a block of bush trees, consisting of a row of each of the varieties Cox's Orange Pippin, Rival and Laxton's Superb. Each row contained twenty trees planted at 18 feet apart, of which six served as untreated controls.

Two fungicidal sprays were compared :

(a) <i>Dichloronaphthaquinone</i> (50 per cent.)	..	..	..	0.1%
<i>Epsom salts</i>	..	..	..	0.1%
(b) <i>Phenyl mercury chloride</i> (Formulation "C") (equivalent to 0.005 per cent. pure material)	..	..	..	0.2%
<i>Methyl ethyl cellulose</i> (2 per cent.)	..	..	..	1%

No wetting agent was added, and the apple fruits were fairly easily wetted. Spraying was carried out on 12th July and 16th August, 1950, under favourable conditions, at the rate of $3\frac{1}{2}$ to 4 gallons per tree. On each occasion no rain fell during the ensuing 18 hours.

During winter pruning, all mummified fruits had been removed from the 280 trees on the plot. Throughout the summer months, all fruits infected with brown rot were removed regularly from the trees in the rows adjacent to those of the trial.

In view of the well-known susceptibility of Laxton's Superb to brown rot, this variety was used for detailed recordings of infection; fruit infection was recorded weekly from mid-August, on samples of approximately 100 fruits on each of five trees per treatment. On 3rd October, 1950, when the fruit was picked, an estimate was made of the number of healthy fruits which had been damaged in each sample. Table II summarizes the results obtained, together with estimates of the total brown rot loss, based on the assumption that fruits in contact with primary infections would ultimately have succumbed to the disease.

TABLE II.

Brown rot infection of Laxton's Superb apples, August to October, 1950.

Treatment	Total no. fruits recorded.	No. with uninfected injuries.	No. with infected injuries.	Estimated brown rot loss (%).
Dichloronaphthaquinone (50%)	501	24	1	0.2
P.M.C.	500	17	12	6.2
Control	493	36	13	5.4

The data indicate that application of the quinone was followed by a substantial reduction in infection of injuries, with a corresponding decrease in estimated total

loss. Phenyl mercury chloride afforded no control. It should be stressed that the brown rot attack was a light one.

PHYTOTOXICITY.

Both phenyl mercury chloride and dichloronaphthaquinone were liable to cause injury to apple and plum fruit. Slight damage was caused by phenyl mercury chloride-kaolin preparations, at concentrations of 0.0035 per cent. to 0.005 per cent. of active material, to fruits of Victoria plums and Cox's Orange Pippin and Laxton's Superb apples. The damage was confined to those parts of the fruits on the underside of the truss, presumably due to the accumulation of spray residues by drainage (Plate I, Fig. 1).

Dichloronaphthaquinone at concentrations of 0.0375 per cent. to 0.05 per cent. resulted in fruit spotting on Victoria plums and slight green blotchiness on three varieties of apple. The addition of magnesium sulphate tended to reduce, but not prevent, damage. Plate I, Fig. 2, shows typical dichloronaphthaquinone damage on Victoria plum.

No leaf damage resulted from either spray.

METHODS OF ESTIMATION OF INFECTION.

The aim of the research was to seek a control for brown rot of apples and plums by applying a fungicidal summer spray; and, in order to assess the merits of the treatment, a reliable method of recording fruit infection was clearly necessary. Critical examination of experimental data suggests that the method generally used in the past, and adopted in the earlier part of these studies, is statistically unreliable. It entailed recording the proportion of infected fruits in a 200-250 sample per tree and, in a trial on plums in 1948, much tree-to-tree variation was shown by the resulting data. To reduce it in 1949, a constant number of mummified fruits per tree was supplied as inoculum, before spraying, but with little success.

From first principles it seems illogical to express infections as a proportion of total fruits sampled, because undamaged fruits are practically immune from primary infection (Wormald, 1935, pp. 21, 30), and for 1950, therefore, this method was modified by including the number of uninfected fruits with skin damage, and also recording primary and contact infections separately.

From the detailed recordings of brown rot infection in Table I, values of χ^2 and corresponding values of P for tree-to-tree variability were calculated in two ways:

(a) By the original method of recording, analysing the proportion of the total fruits found to be infected.

(b) By the modified method, analysing the proportion of total injured fruits sampled which showed primary infections. The total number of injured fruits was considered to be the sum of the number of injured healthy fruits and the number of fruits showing primary infections, since it can be assumed that such infections developed at injuries.

Table III shows the values obtained, together with those similarly derived from infection recordings in a winter spraying experiment (Byrde, 1952b, Table III).

These results suggest that a considerable decrease in tree-to-tree variability of data has resulted from the modified technique of recording fruit infection.

Analysis of the data available on total numbers of injured fruit shows that in neither of the above experiments does injury follow a normal distribution from

TABLE III.

Values of χ^2 and P in two experiments, as obtained by two methods of analysing infection.

Source of data.	Method.	χ^2	Degrees of Freedom.	P
Table I (this paper)	(a)	62.788	10	<0.001
	(b)	15.663	10	0.2-0.1
Table III (Byrde, 1952b) ..	(a)	43.497	9	<0.001
	(b)	12.606	9	0.2-0.1

tree to tree, the value of P for the distribution of injury being less than 0.001 in each experiment. It is to be expected, therefore, that infection data, since they are dependent on the occurrence of injuries, should be heterogeneous with relation to the total number of fruit sampled.

Although no significant difference between treatments could be shown in the winter spraying experiment by the modified technique of recording, it would have been possible to indicate a significant difference had the original method of recording been used. This would have been misleading, and largely due to the fact that the samples of fruit from unsprayed trees suffered more widespread injury. The possibility that the results of 1948 and 1949 have been misinterpreted in a similar way must also be borne in mind.

The statistical data just presented indicate the importance of taking account of injured fruit when recording infection in fungicidal trials against brown rot, particularly when the samples used are comparatively small.

In the case of apples, the problem is further complicated by the fact that fruits infected in the earlier part of the season frequently drop off before the crop is finally picked. Any recording of infection at picking time alone, as mentioned by W. C. Moore (1943), is therefore of limited value, especially as fungicidal treatments are generally applied several weeks before harvest, and might thus be expected to control the earlier infections more successfully than the later ones. The method of weekly recordings used by M. H. Moore (1950a) overcomes this difficulty, but it is considered that account should also be taken of healthy injured fruit at the time of picking, when assessing fungicidal sprays against apple brown rot.

EFFECT OF RAINFALL ON DISEASE CONTROL.

In contrast to the results of 1948 and 1949 against brown rot of plum (Byrde, 1949, 1950), those of 1950 were disappointing. A possible explanation lies in the July rainfall of the three years, figures for which are shown in Table IV.

TABLE IV.

July rainfall, 1948-50.

Place of trial.	Year.	July rainfall (in.)	Average July rainfall (in.)
Reading	1948	0.77	2.28
Long Ashton	1949	1.42	3.26
Long Ashton	1950	4.15	3.26

It will be seen that the figures for 1948 and 1949 are below the average, while 1950 shows a marked excess. This heavy rainfall probably washed off the fungicidal deposits rapidly and in this it would be assisted by the high concentration of wetting agent used on 7th July, 1950; 2.66 in. of rain fell during the fifteen days after this spraying, representing a large proportion of the month's total.

SUMMARY.

1. Applications of three organic fungicides in July, 1950, resulted in no significant control of brown rot of plum (caused by *Sclerotinia fructigena* and *S. laxa*). The addition of an excessive concentration of wetting agent to the sprays, coupled with heavy rainfall after spraying, may have contributed to the failure to reduce infection.

2. Two summer applications of 0.05 per cent. 2:3-dichloro-1:4-naphthaquinone to Laxton's Superb apples were followed by a substantial reduction of a relatively light brown rot attack; corresponding treatment with 0.005 per cent. phenylmercury chloride afforded no control.

3. Phytotoxicity was encountered from the use of phenyl mercury chloride and 2:3-dichloro-1:4-naphthaquinone, particularly on plums.

4. Evidence presented suggests that a marked reduction in tree-to-tree variability in the records of brown rot infection of plum fruits can be secured by a modified technique of disease recording. This takes into account the extent of fruit injury, at the same time differentiating between primary and contact infections.

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The sample of 1-phenyl-3-5-dimethyl-4-nitroso-pyrazole (J.55) was kindly synthesized by Dr. D. Woodcock, of Long Ashton Research Station.

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PLATE I.

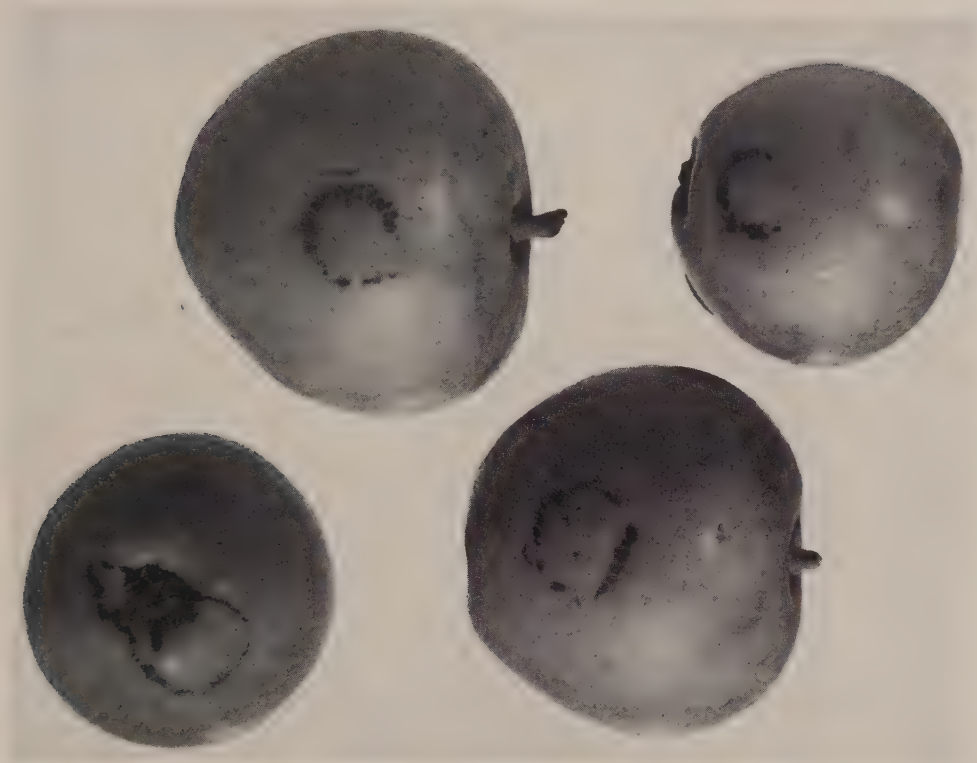


FIG. 1.

Spray damage on Laxton's Superb apples caused by phenyl mercury chloride-kaolin preparation, containing 0.005 per cent. active material.

PLATE II.



FIG. 2.

Spray damage on Victoria plums caused by 0.05 per cent. dichloronaphthaquinone.

MOLYBDENUM AS A PLANT NUTRIENT

I. THE INFLUENCE OF MOLYBDENUM ON THE GROWTH OF SOME *BRASSICA* CROPS IN SAND CULTURE

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INTEREST in the practical importance of molybdenum in the nutrition of *Brassica* crops began with the discovery by Davies (1945) that symptoms of the long known and widely distributed disorder called Whiptail in cauliflower and broccoli were rectified by soil applications of micro-nutrient mixtures containing molybdenum. Prior to the commencement of the work to be described here, few clear examples of the essentiality of molybdenum for higher plants were known. The water culture experiments of Arnon and Stout (1939) with tomato, of Piper (1940) with oat and fo Warington (1946) with lettuce, provided the main evidence for this conclusion. Hewitt and Jones (1947) used sand cultures to confirm the results obtained with tomato and showed in addition that certain *Brassica* species were also sensitive and interesting indicator plants for use in the study of molybdenum nutrition. Since then a survey has been in progress to observe the effect of molybdenum supply on several crop plants, and some preliminary results have already been published (Hewitt and Jones, 1949, 1950). This paper describes results obtained with some *Brassica* crops which present features of especial interest in relation to molybdenum. Effects of acute and moderate deficiency on visual appearance and brief reference to results obtained with high molybdenum levels are included.

EXPERIMENTAL.

PLANT MATERIAL.

Seedlings were raised either by sowing on glass wool and transplanting after about 10 days into the sand cultures or by sowing direct and thinning, or (in later work) by sowing in purified sand and transplanting after 8-12 days with minimum root disturbance. The last method was the most satisfactory as the advantages of "re-setting" *Brassica* seedlings down to cotyledon level were combined with good germination conditions, least disturbance of the roots and minimum contamination. Swede seeds were always sown direct in the cultures and thinned as necessary. Four to six plants were left in each of the deficient cultures and one ultimately in the controls (see Table I).

The following varieties were used: cauliflower (Majestic), rape (Black), savoy cabbage (Ormskirk Medium), kale (Marrowstem Green), kale (Hungry Gap), brussels sprouts (Rous Lench), swede (Purple Top).

METHODS.

A full account of the efficient standardized procedure devised for this work and a discussion of related methods are given in papers by Hewitt (1952) and Hewitt and Hallas (1951). Brief details only, therefore, are given here.

Containers were 5 l. or 1.5 l. Pyrex beakers, with a basal drainage hole. They were cleaned first with hot water and a detergent, followed by immersion in concentrated HCl and finally by steaming. The drainage hole was covered by acid-extracted glass wool and a watch glass.

Silica sand from Leighton Buzzard was used. The "available" molybdenum content, estimated by the *Aspergillus niger* method (Hewitt, 1950), was 0.001-0.002 p.p.m., i.e. about one-tenth of the total acid-soluble fraction. The sand was purified with hydrochloric and oxalic acid as described by Hewitt (1947). Three 7-hour periods of treatment were satisfactory. In 1950 an additional alkaline treatment with 0.25 per cent. NaOH, 10 per cent. Na₂CO₃ 10 H₂O and 0.17 per cent. Permal B.X. surface-active material was included. Sand was leached between each treatment and air pockets were avoided when filling the containers. Leaching with purified 0.02 M Ca(NO₃)₂ solution was continued until the leachate contained less than 0.00001 p.p.m. Mo and all exchangeable H⁺ ions were removed (Hewitt, 1947). The purified sand contained about 0.00002 p.p.m. available molybdenum as determined by *A. niger* in 1949 and probably less than 0.00001 p.p.m. in 1950.

Basal (macronutrient) stock solutions (1 or 2M.) were prepared with A.R. grade salts twice recrystallized from 50 per cent. alcohol, or with calcium nitrate prepared as described by Hewitt (1947).

Solutions used in 1948 were purified by co-precipitation of molybdenum with iron and 8-hydroxyquinoline as described by Hewitt and Jones (1947). From 1949 co-precipitation by copper sulphide (Stout and Meagher, 1948) was used. Tests with *A. niger* (Hewitt, 1950) showed it to be equally efficient and simpler than the 8-hydroxyquinoline method. H₂S was passed rapidly for 30 minutes through the solutions containing 500 p.p.m. Cu (as sulphate).^{*} After standing overnight the precipitate was filtered through a No. 4 porosity Pyrex glass sinter. The filtrate was tested with hydrogen sulphide and the process repeated if necessary. The filtrate was heated to expel H₂S, re-filtered, and made to volume in Pyrex bottles.

Introduction of significant contamination by iron compounds is likely. Their effective purification for molybdenum deficiency studies was not undertaken until the work of Hewitt and Jones (1947) and Evans *et al.* (1950). The method outlined here removed copper, zinc, manganese and gallium as well as molybdenum and was used by Hewitt and Jones (1949).

A.R. grade FeSO₄ (NH₄)₂ SO₄ 7 H₂O was twice recrystallized, extracted first with 8-hydroxyquinoline (oxine) in CHCl₃ at pH 2.8 and then by 6N HCl and ether. The iron was oxidized by purified H₂O₂; ferric chloride was extracted into ether from 6N HCl, and restored to the aqueous phase in glass-distilled water. Ferric citrate was prepared by evaporation with citric acid (purified by recrystallization and copper sulphide precipitation).

Water was distilled from tinned copper stills with silver condensers, redistilled from Pyrex glass stills and stored in Pyrex carboys. The molybdenum content was 0.00006 p.p.m. after the first distillation and 0.000003 p.p.m. after the second (Hewitt, 1950). Care was taken to avoid contamination of water siphons by stock bottles. Water supplies for molybdenum deficient and other treatments were kept separate.

The nutrient solutions had the following composition as m. eq./l. Ca(NO₃)₂ 8-10;

^{*} It is desired to correct here an error in the report by Hewitt and Jones (1950), where the Cu concentration was given as 50 p.p.m. instead of 500 p.p.m. actually used.

KNO_3 3.4; NaH_2PO_4 (as PO_4''') 4; MgSO_4 3; Fe''' (as citrate) 0.3; Mn'' (as sulphate) 0.02; Cu'' , Zn'' (as sulphates) 0.002; B''' as H_3BO_3 0.15; Co'' and Ni'' (as sulphates) 0.0002; Ga''' (as nitrate) 0.0002.

Molybdenum was omitted entirely from the deficiency cultures and the minimum absolute concentration here was estimated to be about 0.000003-5 p.p.m. in solution and an additional amount up to 0.00001 mg/Kg of sand. In 1948 when less-effectively treated sand was used the minimum amount available was probably about three to six times this amount. The normal concentration given to control cultures was 0.02 p.p.m. (0.0012 m.eq. Mo^{VI}) and to "high" molybdenum treatments 4.8 or 9.6 p.p.m. (0.3-0.6 m.eq. Mo^{VI}).

RESULTS.

VISUAL EFFECTS.

These are most conveniently presented as a summary of typical effects, followed by notes on each variety in turn, in chronological order of appearance. Variations in behaviour noted below occurred in relation to varied efficiency of technique in different years. In all instances growth was severely reduced, compared with controls, as shown by the yields in Table I.

The visual symptoms of molybdenum deficiency in different *Brassica* crops showed marked similarity. The characteristic features which appeared during the first few weeks of growth included mottling, leaf cupping, grey tinting, marginal limpness and membranous texture. Rapid wilting and scorching of the old or middle expanding leaves occurred in seedling stages or under more severe deficiency conditions. Cotyledons frequently remained green and turgid for a considerable period during the appearance of leaf symptoms. Plants remained severely dwarfed until killed.

Symptoms in more mature plants after partial recovery, or when less acute deficiency prevailed, were entirely different in appearance. Younger leaves were then affected most and characteristic malformations, loss of lamina, leathery texture and death of the growing point occurred. There were, as might be expected, exceptions to the general behaviour. Thus leaf-cupping did not occur in rape and Hungry Gap kale. Abnormal development of young leaves was not recorded in brussels sprouts, rape or Marrowstem kale, but premature death of the growing point (presumably a related effect) was common in the latter and leaf distortions have been found by Plant (1950, 1950a) in brussels sprouts in the field under suspected conditions of molybdenum deficiency.

Reproducibility of visual effects from one year to the next, especially during the initial period, was noteworthy. Subsequent (secondary) effects which developed showed more variation but plainly were basically similar in nature. Root systems were weak and brown when deficiency was acute but no striking effects were noted. Examples of typical effects recorded here are illustrated in the plates.

Cauliflower plants given excess molybdenum (5-10 p.p.m.) in 1948 and 1949 did not show outstanding symptoms. In both years transient effects suggestive of slight ammonia toxicity were observed. These included a blue-grey tint just within margins of old leaves followed by yellowing and bronzing and intervenal scorch. Yields suggested that growth was actually greater and this has been confirmed at Long Ashton by S. C. Agarwala (1951). In a preliminary test in 1947 during the winter, cauliflower and savoy cabbage plants showed symptoms of chlorosis in expanding leaves, suggestive of iron deficiency.

TABLE I.

Effects of molybdenum level on yield and mortality of Brassica crops in sand culture.

Crop.	Year.	Duration of experiment in weeks.	Treatment.	No. of plants in cultures.	Average dry weight per plant (in gm.). A = Aerial parts. T = Total yields.	Approx. % killed after 8½ weeks.
Brussels sprouts	1949	15	-Mo	18	0.2 } A	25
	1950 1st sowing	22	+Mo	1	66.5 } A	
	1950 2nd "	11	-Mo	6	0.16 } A	
Cauliflower	1949	15	-Mo	4	0.12 } A	20
	1950	33	+Mo (normal) Mo (excess) -Mo	8 8 4	1.3 } T 187.2 } T 258.0 } T 2.9 } T	
	1949	15	-Mo +Mo	6 2	0.6 } A 45.7 } A	
Hungry Gap kale	1949	15	-Mo +Mo	5 1	4.3 } T 132.3 } T	40
	1949	15	-Mo +Mo	5 1	4.3 } T 132.3 } T	
Swede	1949	20	-Mo	2	All -Mo plants killed in 10 weeks 2.3 } T 55.7 } A 0.18 } A	90
	1950 1st sowing	11	+Mo	2		
	1950 2nd sowing	11	-Mo	4		
Marrowstem kale	1949	15	-Mo	5	17.3 } T	15
	1950	33	+Mo	1	219.7 } T	
	1950	33	-Mo +Mo	3 1	3.6 } T 330.0 } T	
Savoy cabbage	1949	15	-Mo +Mo	4 1	17.0 } T 70.3 } T	5
	1950	33	-Mo (partial recovery) -Mo (no recovery)	1 2	23.4 } T 0.9 } T	
	1950	33	-Mo (partial recovery) -Mo (no recovery)	1 2	23.4 } T 0.9 } T	

*Cauliflower (1948, 1949, 1950).**

Seedlings were pale, diffusely mottled (28 days). Leaves became cupped or incurled at the margins, membranous and limp with greyish tint, scorched, and finally completely withered and papery (30 days). This latter sequence of effects usually developed rapidly in the course of two to four days. The symptoms were most marked in older (but not always the oldest) leaves and usually appeared first in the middle expanding leaves. Sometimes petioles wilted before appreciable scorch appeared in the leaves. Cotyledons remained turgid and green for several weeks after these symptoms appeared. Where the technique was consistently good, scorching progressed to apical leaves and plants remained severely dwarfed. Death of the youngest leaves and growing point and finally of the plant resulted (8-14 weeks) (Plate II, Fig. b).

Plants that had access to traces of molybdenum (accidental contamination, or less effectively purified sand) were larger; intervenal mottling was sometimes sharply defined, leaf margins were still cupped or inrolled; papery intervenal scorching followed more slowly and wilting was less prevalent.

Plants with a functional growing point retained the ability to make rapid recovery, however severe the other deficiency effects. Such recovery readily occurred in a few cultures and normal growth persisted for varying periods followed by appearance of different symptoms when molybdenum was again deficient. The newly developed and normally expanded leaves were green and only slightly cupped, later faintly mottled. Younger leaves, however, showed irregular margins, which were brown and filamentous, or chlorotic intervenal areas mainly in the basal half of the leaf, which later perforated. These leaves developed with irregular, defective or narrow laminae, which were thickened, wavy and often cupped at the margins in places (Plate III, Fig. e). The leaf tip was often dead and ended in a brown stump. Prolonged deficiency at this stage led occasionally to death of the growing point before the youngest leaves started to expand. These became brown and water-soaked and exuded a clear brown fluid before drying up. Older leaves became paler and sometimes finally scorched and dropped off.

A young plant transplanted from complete nutrient to molybdenum deficient cultures, about five weeks after sowing, developed stunted younger leaves with brown margins and incurling laminae as described, but the growing point did not die. Plants transplanted 9 weeks after sowing remained normal.

Savoy cabbage (1948, 1949, 1950).

Early symptoms of acute deficiency were similar to those in cauliflower, but leaf cupping, mottling and the limp, membranous or water soaked appearance prior to scorching, were more marked. The colour was olive green and leaf margins were relatively chlorotic with purple tinted veins. Symptoms appeared about 20 days after sowing and developed first in the oldest leaves; later mid-stem leaves wilted more rapidly. Withering progressed upwards and death of the plants tended to occur suddenly (Plate I, Fig. a, and Plate II, Fig. d).

Initially, savoy cabbage seemed equally or even more sensitive than cauliflower, but it possessed greater powers of recovery and often made considerably more growth

* Dates in brackets indicate years in which the crop was grown; times, in days after sowing, for development of deficiency symptoms are given in the text.

without secondary effects. Sensitivity to low (but not acutely deficient) levels of molybdenum in later stages of development was apparently less.

In 1950, however, a plant that had initially shown practically no symptoms, due presumably to an unsuspected slight contamination, ultimately developed (10 weeks) dull white mottling of the older leaves which were grey-green, thick and leathery in texture. The mottling later disappeared but young leaves became brown and necrotic at the margins. The lamina was deformed or ultimately lacking. Death of the growing point with brown exudation, and browning and shrivelling of rudimentary leaves followed. Old leaves remained green for several weeks and then slowly scorched and shrivelled before falling (Plate III, Fig. a).

Brussels sprouts (1949, 1950 two sowings).

Leaf-cupping was more pronounced than in any others. Mottling, marginal wilting, membranous texture, scorch and withering developed in rapid sequence from the leaf tip, followed by collapse of the petiole and whole leaf. Symptoms first appeared 18-24 days after sowing and progressed steadily to youngest leaves. Death of growing point and of the plants occurred in 10-14 weeks when their height was only about 6-8 cm. Cotyledons usually remained green for several weeks after leaf collapse (Plates I, Fig. b; II, Fig. f). This crop consistently showed scarcely any tendency to recovery and plants steadily deteriorated in marked contrast to others, e.g. savoy cabbage, cauliflower or swede in instances where slight contamination might have occurred. Brussels sprouts was judged to be among the more sensitive crops in sand culture and comparable with swede.

Swede (1948 two sowings, 1949, 1950 two sowings).

Leaves were pale green and lustreless, followed by diffuse yellow-green mottling and slight (sometimes pronounced) cupping (17 days from sowing). A grey tint, rapid incurling of margins, limpness, buff coloured scorch and withering of the whole leaf ensued. Seedlings became totally withered and often died in 4-8 weeks (Plates I, Fig. c; II, Fig. c). In 1948, and in one experiment in 1950, partial recovery occurred. In 1950 the older leaves continued to show scorching and mottling but, in 1948, recovery was more marked and prolonged. Foliage was practically normal for a few weeks and the "root" (hypocotyl) enlarged. Later (1948, 1950) young leaves became brown at the margins and developed with cupped defective laminae and finally only stunted brown-tipped petioles, devoid of any lamina (Plate III, Fig. c).

Rape (1949, 1950).

Leaves were pale green and soon brightly mottled yellow-green with a sharply defined vein pattern (20 days after sowing). Leaf cupping did not occur. Margins inrolled, wilted, scorched and finally withered completely (about 28 days) (Plate II, Fig. e). Oldest leaves occasionally persisted for a longer period and became thickened and somewhat rubbery in texture with an orange or yellow tint around the margins. The habit was often rosette. Plants were killed in 12-20 weeks as the symptoms progressed. Tendency to recovery was less than for savoy cabbage, cauliflower and kale. On the other hand, growth persisted in the dwarfed plants for a much longer period than in swede or sprouts although initial sensitivity was comparable.

Kale (Hungry Gap) (1949).

The early behaviour of this crop was practically identical with rape, but many plants were killed in 6-9 weeks (Plate I, Fig. d). Also, tendency to recovery was greater and in some cultures normal growth resumed for a short period. Deficiency effects reappeared after 2-3 weeks and younger leaves were then deformed, narrow or lacking lamina, and dead at the leaf tip in manner similar to swede (Plate III, Fig. b).

Kale (Marrowstem) (1948, 1949, 1950).

Seedlings were pale grey-green, then mottled diffusely yellow-green, especially nearer leaf margins. Cupping and inrolling of wilted margins (20 days after sowing) was followed by pale scorching and leaf withering (30 days). Collapse of petioles was seen occasionally. Cotyledons tended to remain green. Middle leaves were affected before the oldest ones (Plates I, Fig. e; II, Fig. a).

Kale also showed considerable powers of recovery. In 1948 and 1949 secondary symptoms occurred after temporary recovery. The youngest leaves became brown and death of the growing point followed. Abnormally shaped leaves, however, did not develop. Older leaves finally scorched and plants were killed (Plate III, Fig. d). In 1948 an axillary bud regenerated the growing point and recovery persisted to the end of the experiment.

EFFECTS OF MOLYBDENUM ON GROWTH.

The relative effects on overall growth are illustrated by the yield data of Table I, mainly based on work carried out in 1949. In many instances the deficient plants were dying when harvested, others had made partial recovery. The results represent the relative response of small populations of plants, each showing varied resistance to unfavourable circumstances. The species of *Brassica* as a group are obviously especially sensitive to lack of molybdenum. The relative sensitivity of the different varieties to molybdenum deficiency was assessed from yield data and on a basis of visual behaviour with respect both to early growth and powers of recovery.

Thus in respect both of initial behaviour and yield, brussels sprouts and swede appeared highly sensitive under culture conditions, whilst savoy cabbage and Marrowstem kale were consistently the most resistant. Hungry Gap kale, rape and cauliflower were intermediate both as regards their powers of recovery and overall yields.

NITRATE ASSIMILATION.

Hewitt and Jones (1947, 1949), Mulder (1948), Stout and Meagher (1948) and Wilson and Waring (1948) have shown that higher plants deprived of molybdenum are unable readily to assimilate nitrate nitrogen, and oxidizing materials accumulate in the foliage. The concentrations given in Table II are relative, as the diffusion tissue test method of Plant *et al.* (1945), used here, indicated only some proportion of the total nitrate content and the data were determined on petioles and not laminae. As the technique was used in a standardized form, however, the comparisons for crops and seasons are probably valid. The results have been subsequently confirmed quantitatively by Agarwala (unpublished work).

TABLE II.

The effect of molybdenum supply on nitrate content of leaf petioles.

Crop.	Time.	Nitrate as p.p.m. in Morgan's Extract.	
		—Mo.	+Mo.
Cauliflower petiole	3 p.m. 6/7/48	80	2
	11 a.m. 29/7/48	200	5
Swede (mature) petiole	11 a.m. 23/6/48	200	60
	11 a.m. 4/8/48	160	Nil
Swede seedlings	15/9/48	210	20
Marrowstem kale petiole	11 a.m. 23/6/48	50	5
	8 p.m. 16/7/48	10	Nil
Savoy cabbage petiole	8 p.m. 16/7/48	360	70
	11 a.m. 24/7/48	150	Nil
	3 p.m. 12/8/48	30	Nil

DISCUSSION.

The visual symptoms shown by *Brassica* crops are plainly similar. The sudden wilting, membranous texture and scorching of leaves suggests that water relations are disturbed. Measurement of transpiration losses under controlled conditions would be of interest. Osmotic pressure values, recorded for leaf epidermal cells of deficient plants by Hewitt and Jones (1947, 1949), were also increased. This effect is consistent with the accumulation of nitrate or possibly other metabolites.

The role of molybdenum in the assimilation of nitrate is now generally accepted, but it will not be discussed at length here. It is noteworthy, however, that although *Brassica* crops are regarded as having high nitrogen requirements, lack of molybdenum does not induce typical symptoms of nitrogen deficiency as seen in these crops. This may be due in part to the abnormally high concentrations of unassimilated nitrate present in the foliage. This condition may even possibly be a contributory factor in the excessive scorch and leaf withering effects recorded above.

The evidence of visual symptoms and yields indicated that there was an appreciable difference in the relative susceptibility of the various species grown. Swede and brussels sprouts were more susceptible and savoy cabbage and Marrowstem kale rather less so than the rest. The ability to make some recovery from initial deficiency varied greatly and this merits further study. It is tentatively suggested (from unpublished data) that the degree of root development was related to this property. Leaf-cupping was partly related to the leaf shape and was less evident in types with irregular leaves, e.g. rape.

An outstanding feature of the response of *Brassica* crops, so far studied, to molybdenum deficiency is the tendency for death of the growing point or malformation of young leaves whilst older ones remain more or less normal. This particular response has not been recorded in any species outside this genus. An important factor in the incidence of such symptoms appears to have been the introduction (accidentally or purposely) of undetermined but relatively small and ultimately

inadequate amounts of molybdenum during the initial or intermediate stages of normal development. These effects would be consistent with the suggestion that molybdenum is partially immobilized in older leaves after a certain period. The younger tissues would then show later effects of shortage. Restricted supply to the developing leaves of an essential metabolite could have a similar effect, as also could a change in the relative molybdenum requirement after a certain stage of growth. Analytical data relevant to these points will be presented later. Differences in molybdenum content between young, middle and old leaves are not great, however, and a final conclusion is not yet possible.

The condition recognized as Whiptail in cauliflower and broccoli is now associated with molybdenum deficiency in the field. The earlier observations of Davies (1945) and Mitchell (1945) that applications of molybdenum compounds or liming mitigated the disease have been fully confirmed by Waring, Shirlow and Wilson (1947) and Waring, Wilson and Shirlow (1948) in Australia, and by Plant (1950, 1950a, 1951), and Jones and Dermott (1950) in England. Cauliflower plants showing features clearly suggestive of the Whiptail condition were first produced in sand culture experiments by Hewitt and Jones (1947). Since then, similar effects have been demonstrated in swede, Hungry Gap kale and Marrowstem kale and savoy cabbage, either as malformation of younger leaves, or death of the growing point. Savoy cabbage and brussels sprouts are also known to show similar leaf malformations under field conditions in acid soils (Plant, 1950, 1950a, 1951), but these have not yet been recorded for swede or the kales. Recently, however, Waring (1950) reported that "young-leaf edge-burn" in swede-turnip and also in cabbage, broccoli and sprouts is due to molybdenum deficiency in some Australian acid soils.

In the work described here the incidence of Whiptail-like symptoms was somewhat sporadic and unpredictable in development. A consistent feature, however, appeared to be partial recovery of initially affected plants. Under field conditions where Whiptail occurs, a number of diverse but characteristic effects have been observed. These have been fully described by Plant (1950, 1950a, 1951) and by Waring, Wilson and Shirlow (1948). They include death of the growing point; weak or abnormal curd; malformed leaves, which are either vestigial or stunted, with pronounced marginal and intervenal crinkling, or are narrow, irregularly scalloped and seemingly abnormally elongated. They are sometimes mainly, or even entirely, devoid of lamina. In several instances affected plants have unusually large old leaves, and the foliage of Whiptail plants is generally dark green and rubbery in texture. More rarely in this country (Plant, 1951) and sometimes under Australian conditions (Waring, Wilson and Shirlow, 1948; Waring, 1950) mottling and scorching of the foliage occurs before Whiptail symptoms develop.

The dark green plants with large old leaves are the result of initially vigorous growth frequently observed prior to the onset of Whiptail, and indicate that considerable nitrogen assimilation must have occurred. Such plants, bearing numerous elongated middle leaves with narrow, irregular, scalloped margins, were not reproduced in these experiments. Whiptail symptoms, typical in all respects of field plants, have more recently been reproduced in sand cultures at Long Ashton and the necessary conditions elucidated (Hewitt and Agarwala, 1951).

The biochemical and histological factors leading to the production of defective laminae and death of the growing point are still obscure. It was suggested by Hewitt, Jones and Nicholas (1948) that excess manganese (a frequent occurrence in acid

soils) might be partly conducive to the condition in the field. Unpublished analyses by one of us (E.J.H.) have shown that manganese may depress the uptake of molybdenum by plants and an antagonistic relation between these elements has also been found to apply to the amino-acid content of the cauliflower and other crops by Hewitt, Jones and Williams (1949). The experiments with Agarwala just mentioned indicate, however, that excess manganese is not important under culture conditions. Wilson and Waring (1948) considered that nitrate accumulation or non-assimilation might be a contributory cause. Hewitt and Jones (1950) pointed out that the abnormal leaf shape produced might indicate a disturbance in some hormonal control of leaf development and that metabolites other than nitrate might accumulate, or be depleted, with lack of molybdenum. Since then, Hewitt, Agarwala and Jones (1950) have shown that ascorbic acid is greatly reduced in molybdenum deficient plants. As, however, the effect on ascorbic acid is widespread among different genera it does not at present offer an obvious clue to the sensitivity of *Brassica* crops to Whiptail and related effects. The elucidation of this aspect of molybdenum nutrition of *Brassica* is now receiving further investigation.

SUMMARY.

1. An efficient sand-culture technique for the production of acute molybdenum deficiency in plants has been developed; purification methods and molybdenum contamination are checked by bioassay with *Aspergillus niger*.

2. A survey of the visual effects of molybdenum deficiency was carried out over three years with seven *Brassica* crops. All were shown to be highly sensitive to molybdenum deficiency.

3. Relative susceptibility to initial deficiency, ability to recover and effect on ultimate yield differed somewhat for the crops examined. A provisional order of decreasing susceptibility in sand culture based on these criteria was as follows: brussels sprouts, swede, cauliflower, rape, Hungry Gap kale, Marrowstem kale, savoy cabbage.

4. Growth was greatly reduced by deficiency, often to about 4 per cent. or less of control plants, but toxicity (to cauliflower) was not marked at 10 p.p.m. Mo.

5. Visual symptoms in early stages were similar for most species and included mottling, scorching, wilting and frequently leaf-cupping of older and middle leaves. Symptoms in later stages often showed a marked change, especially after partial recovery, and developed mainly in young leaves. Malformations, or death of the growing point, were recorded in cauliflower, swede, savoy cabbage, Marrowstem kale and Hungry Gap kale, but not in rape or brussels sprouts.

6. The relation of these effects to the field disorder known as Whiptail in cauliflower and broccoli is discussed, and possible contributory factors are reviewed in relation to the role of molybdenum in plant growth.

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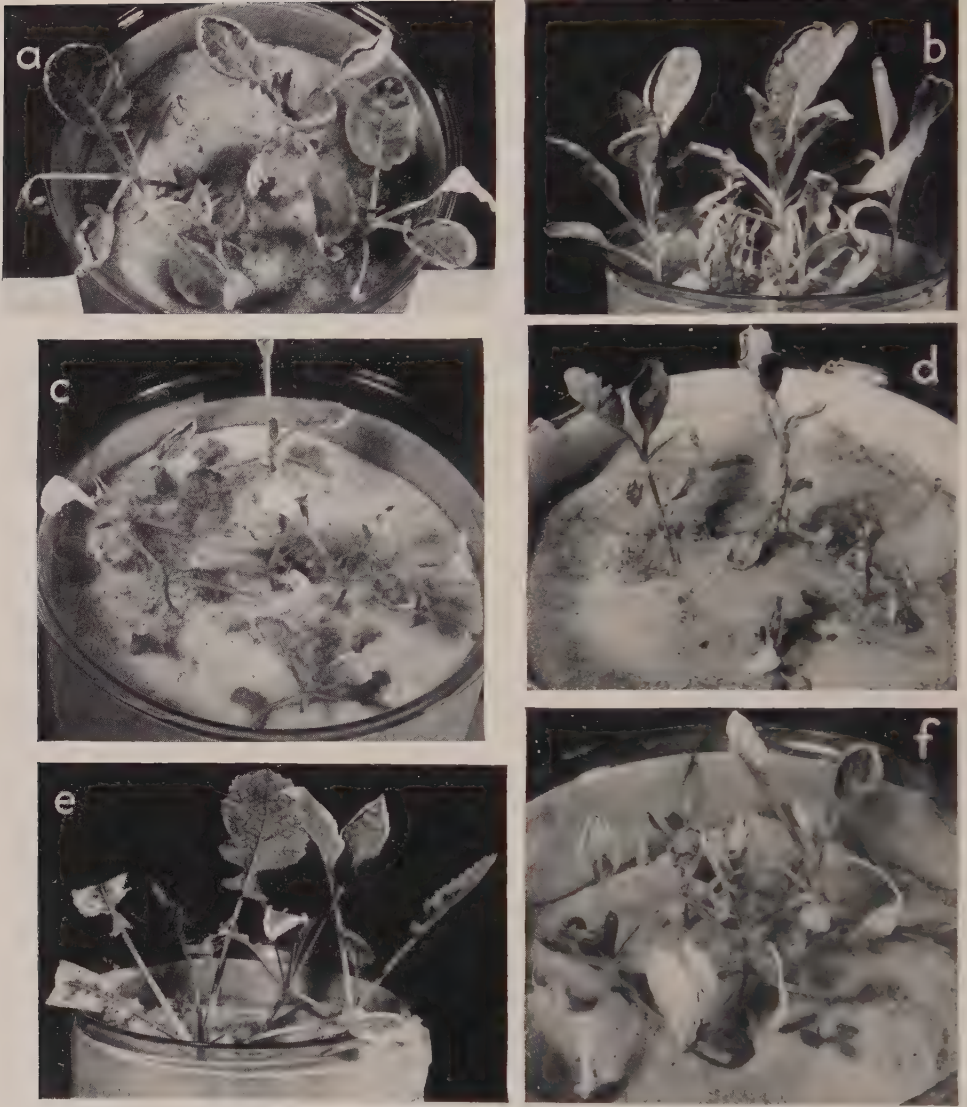
PLATE I.



Comparative effects of molybdenum deficiency on growth of *Brassica* crops ; age 6 or 7 weeks from sowing.

FIG. (a), Savoy cabbage. (b), Brussels sprouts. (c), Swede. (d), Hungry Gap kale. (e), Marrow stem kale (17 weeks).

PLATE II.



Detail of molybdenum deficiency symptoms in seedling stages of growth; age 6-9 weeks.
FIG. (a), Marrowstem kale. (b), Cauliflower. (c), Swede. (d), Savoy cabbage. (e), Rape.
(f), Brussels sprouts.

PLATE III.



Secondary effects of molybdenum deficiency in adult plants.

FIG. (a), Savoy cabbage. (b), Hungry Gap kale. (c), Swede. (d), Marrowstem kale. (e), Cauliflower.

MOLYBDENUM AS A PLANT NUTRIENT

II. THE EFFECTS OF MOLYBDENUM DEFICIENCY ON SOME HORTICULTURAL AND AGRICULTURAL CROP PLANTS IN SAND CULTURE

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THE previous paper in this series by Hewitt and Jones (1952) described deficiency effects in *Brassica* crops. In this paper visual results observed in other crops during the same period (three years) are described. As already pointed out (*loc. cit.*) the technique steadily improved during the time considered, and symptoms produced in later work (1949, 1950) were often more acute than those in 1948, a preliminary account of which was published by Hewitt and Jones (1949). An indication of relative susceptibility was obtained, however, by the inclusion each year of a few indicator crops of known behaviour such as *Brassica* spp. and tomato.

EXPERIMENTAL.

The crops and varieties used were as follows: tomato (Market King), lettuce (All Year Round), mustard (White), sugar beet (Webb's no. 2), Alsike clover, red clover (Dorset Marl), lucerne (Grimm strain), pea (Onward), dwarf bean (Masterpiece), broad bean (Long Pod), barley (Plumage Archer), oat (Red Algerian), rye, perennial rye grass (Aberystwyth S.23), cocksfoot grass (S.37), Yorkshire fog (*Holcus lanatus*), celery (Giant White), flax (Liral Prince).

Seeds were sown direct in the sand in most instances. In some tests, tomato, beet and lettuce were raised on acid-extracted glass wool or purified sand and transplanted into the cultures. The effect of removing the cotyledons or endosperm from peas, beans and cereals was also tested in 1948. Several seeds were sown and seedlings were thinned soon after germination.

Crops were grown in Pyrex glass containers of 1.5, 5 or 10 l. capacity. Sand was purified as described by Hewitt (1952), Hewitt and Jones (1952). It was treated for three periods of $3\frac{1}{2}$ hours each in 1948, and for four periods of 7 hours in 1950, of which one was with alkali instead of acid. Sand used for tomato in 1949 was given varying periods of treatment from one to three days with acid, or acid and alkali. Glass-distilled water was used throughout. Methods for purification of nutrient reagents, including ferric citrate, are described by Hewitt and Jones (1952) and in greater detail by Hewitt (1952).

The nutrient composition was the same as previously, nitrogen being given entirely as nitrate.

VISUAL SYMPTOMS.

Tomato (1948, 1949, 1950 two sowings).

Symptoms were similar to those recorded by Hewitt and Jones (1947), but severity was greatly accentuated. Paling and intervenal yellowing of expanding

leaves developed 18 days after sowing. This was rapidly followed by curling up at leaf margins and paler brown scorching and withering from leaf tips; symptoms appeared first in the apical leaflet. Finally leaves withered completely and dropped when the plants were only 28 days old. Old leaves were affected first but symptoms progressed until the youngest leaves were involved (Plate I, Fig. b); death of the growing point and of the whole plant occurred in 3-4 months when 10-15 cm. high. In those instances in 1948 when some recovery occurred, symptoms still continued to appear first in the oldest leaves. Cotyledons always remained relatively normal for several days after the first leaves had withered.

Lettuce (1950 two sowings).

Leaves were small, pale (faded) yellow-green (15 days). This stage was followed by yellowing, inrolling and scorching at margins, and finally by complete withering and death of plants (30-35 days) (Plate I, Fig. a). Symptoms commenced in the oldest leaves and progressed to the youngest. Cotyledons did not remain green and fresh as recorded for most *Brassica* crops, tomato and sugar beet.

Mustard (1949).

Symptoms resembled those described by Hewitt and Jones (1947). Foliage was pale green, slightly mottled intervenally, later scorched at margins and finally withered. Plants were more succulent than controls. Oldest leaves were less affected by scorching than middle leaves, in contrast to more general distribution in 1947.

Sugar beet (1948, 1950).

In 1948 expanding leaves were mottled pale yellow-green, older leaves had a faint reddish tint around margins, which curled forward; buff scorching spread from leaf tips towards base (43 days). Plants readily recovered.

In 1950 symptoms were greatly accentuated. Expanding leaves were pale green, somewhat narrow in form, later yellow green; older leaves wilted near the tip or in the petiole, curled up or twisted, scorched and withered. Cotyledons remained large, green and turgid. Symptoms progressed into youngest leaves which blackened; death of growing point and of the plants occurred in 7-9 weeks (Plate I, Figs. c and d).

Alsike clover (1948, 1950).

Growth was markedly reduced. Foliage became dull and pale; leaf margins or intervenal areas were grey-green, margins curled forward and rapidly scorched, or "hatched" intervenally. Leaves finally completely withered and petioles collapsed (6-7 weeks) (Plate II, Figs. b and c).

Red Clover (1948).

Symptoms closely resembled those for Alsike; leaf margins usually curled under, were more chlorotic and scorch more red-brown (6-7 weeks) (Plate II, Fig. a). The effects were similar to those reported by Warington (1950).

Lucerne (1948).

Growth was reduced; middle and younger leaves showed most symptoms. Foliage was dull, pale green with grey tint around leaf tip and margins; intervenal hatching near leaf tip (26 days) was followed by bleaching to white; leaf tip and

margins became limp and irregularly curled upward ; leaves scorched and finally totally withered, petioles wilted and withered ; flowering was greatly reduced (5 weeks) (Plate II, Fig. d). Symptoms were confirmed by Evans *et al.* (1950), in culture experiments using crushed Pyrex glass as an aggregate.

Pea (1948).

Old leaves paled and withered prematurely ; flowering and seed formation were reduced. Removal of cotyledons soon after germination made no visible difference to symptoms.

Dwarf bean and Broad bean (1948)

Foliage was paler than controls and suggestive of nitrogen deficiency, but no distinct symptoms appeared. There was no visible difference due to removal of cotyledons.

Barley (1948, 1950).

In 1948 symptoms were mild. Foliage was lustreless and grey green ; leaf tips became ivory or pale brown ; grain was reduced but not total weight, susceptibility to mildew was apparently accentuated. Removal of the endosperm did not produce any visible difference in symptoms.

In 1950 effects were more acute. The habit was straggling, stems were weak and dry weight much reduced. Foliage was dull, pale green, leaf tips and margins developed grey tinted areas rapidly leading to buff scorch, especially in middle leaves and less acutely in younger leaves (5 weeks), leaf tips wilted. Leaf tip scorch extended intervenally as irregular necrotic areas, leaving faded, grey-green "islands" of tissue which more slowly became brown. Youngest leaves frequently remained rolled and chlorotic and had a constriction close behind the tip or were practically vestigial (10 weeks). Many tillers collapsed, due to wilting below last leaf, or failed to produce further leaves, presumably due to death of the growing point. Ear formation was greatly reduced and grain totally suppressed.

Oat (1948).

Growth was reduced ; plants showed an erect, "spiky" habit ; foliage was pale green with grey lesions between veins, becoming brown, or with orange-red flecks resembling symptoms produced in water culture experiments by Piper (1940). Later, slight intervenal chlorosis, and orange- or red-brown scorch of older leaves starting at leaf tips was observed (11 weeks).

Rye (1948).

Growth was reduced ; foliage was pale yellow-green, with grey tint later ; leaves developed white tips and irregular bleached areas along blade (12 weeks).

Perennial rye grass (1948) ; Cocksfoot grass (1948) ; Yorkshire fog grass (1948).

Growth was reduced to 60-70 per cent. of controls ; foliage was pale yellow-green as though lacking nitrogen ; extensive withering or bleaching in older leaves, commencing from leaf tips, followed (10 weeks).

Celery (1948).

Growth was much reduced ; foliage was initially pale yellow green, and later showed bright yellow chlorosis, generally suggestive of acute nitrogen deficiency.

Flax (1948).

Foliage was pale dull green; younger leaves were yellow-green at tips; browning then spread over the whole leaf (5 weeks). Older and middle leaves were buff tinted (11 weeks), later withering; flowering was reduced, pedicels wilted 2.5 cm. behind flower or bud, but the intervening part remained green; finally withering of whole inflorescence.

EFFECT OF MOLYBDENUM DEFICIENCY ON GROWTH.

Yield data in Table I indicate the extent to which growth of some crops was reduced by lack of molybdenum. Depression of growth was less acute in 1948 than

TABLE I.

*Effect of molybdenum deficiency on growth of crops in sand culture.**

Crop.	Part.	Fresh weight.			Dry weight.		
		—Mo.	+Mo.	ratio %	—Mo.	+Mo.	ratio %
Tomato 1949	Whole plant						
	1st sowing				1.05	12.5	8.4
	74 days						
	2nd sowing				0.33	9.7	3.4
	56 days						
Sugar Beet 1948 ..	Root 148 days	89.0	181.0	49.2	20.6	36.0	57.2
Red Clover 1948 ..	Tops 145 days	138	435	31.7			
Alsike Clover 1948 ..	Tops						
	1st cut 98 days	117	275	42.5	22.4	59.4	37.7
	2nd cut 147 days	166	253	65.6	32.4	55.4	58.5
	Total	283	528	53.5	54.8	114.8	42.7
1950 ..	Tops 49 days	78.8	144	54.7	19.5	39.5	49.4
Lucerne 1948	Tops						
	1st cut 98 days	89.0	148	60.2	20.3	33.3	60.9
	2nd cut 147 days	96.6	142	63.1	18.9	28.9	65.4
	Total	185.6	290	63.9	39.2	62.2	63.0
Barley 1950	Whole plants				39.5	130.5	30.3
Oat 1948	Grain and straw	238	584	40.7			
Rye 1948	Tops	280	388	72.1	66.0	97.4	67.7
Perennial rye grass 1948	Foliage						
	1st cut 120 days	215	302	71.1	54.5	81.0	67.2
	2nd cut 147 days	*64.9	86.2	75.3	11.9	16.4	72.5
	Total	279.9	388.2	72.1	66.4	97.4	68.2
Cocksfoot 1948 ..	1st cut 98 days	185	272	68.0	42.7	58.5	73.0
	2nd cut 120 days	70.5	132	53.3			
	3rd cut 147 days	81.2	99.1	81.8	16.3	19.2	84.9
	Total	336.7	503.1	66.8			
Yorkshire Fog 1948 ..	Foliage 120 days	370	440	84.0	79.5	102.0	78.0

* Yields as g. per beaker except where shown* as g. per plant.

in 1949 and 1950. Yields were often not recorded in these latter years as it was necessary to retain plants beyond the stage when yields could be determined. The difference in growth depression in the different years was related to improved technique, and the severity of deficiency effects on growth was obvious.

Comparison with *Brassica* crops (recorded in the preceding paper, Hewitt and Jones, 1952) and visual appearance indicated that dry weight yields of lettuce, tomato and sugar beet in 1950 were probably only about 1 per cent. of controls.

Relative susceptibility was assessed from the comparative responses observed each year in relation to technique and the behaviour of indicator crops. These included tomato and certain *Brassica* crops whose behaviour was sufficiently well established to justify their use in this manner. The general susceptibility (in decreasing order in each group) was tentatively judged to be as follows:

Highly sensitive and comparable to swede and brussels sprouts (cf. Hewitt and Jones, 1952): lettuce, tomato, sugar beet.

Intermediate: Red clover, Alsike clover, lucerne, barley, celery, flax.

Least sensitive: oat, rye, grasses, large seeded legumes.

NITRATE STATUS AND OSMOTIC PRESSURE.

The relative nitrate status of some normal and molybdenum deficient plants was determined by the diffusion method of Plant, Jones and Nicholas (1945). Results given in Table II, showing nitrate accumulation, are consistent with those reported for *Brassica* crops in the previous paper where instances in the literature, in which a similar relationship has been found, were noted. Roots, however, did not show appreciable differences.

TABLE II.

Relative nitrate status and osmotic pressure of plants grown with or without molybdenum.

Crop.	Part sampled and time.	Nitrate status (p.p.m.).		Osmotic pressure (ats.).	
		—Mo.	+Mo.	—Mo.	+Mo.
Sugar Beet	Petiole				
	23.6.48	180	15	19.60	14.55
	16.7.48	160	5		
	4.8.48	160	nil		
	Root				
	20.9.48	40	20		
Celery ..	Petiole				
	29.7.48	400	180		
Tomato ..	Petiole				
	23.6.48	180	nil	6.72	3.36
	7.8.48	55	7		
	Seedlings				
	15.9.48	220	45		
	Root				
	20.9.48	60	80		
Kale ..	23.6.48			9.52	6.16
Swede ..	23.6.58			8.40	6.16

Approximate osmotic pressure values in stomatal guard cells were determined in a few crops. The values were recorded as those just causing visible plasmolysis in glucose solutions graded in concentration by $\cdot 01$ M steps. The results are given in Table II. Molybdenum deficient plants had higher osmotic pressures than the control plants. These results were consistent with nitrate (solute) accumulation. They confirmed earlier observations by Hewitt and Jones (1947).

DISCUSSION.

Wilting, necrosis and scorching of leaves, often preceded by grey tinting, were characteristic features of the visual symptoms of molybdenum deficiency, and analogous features were recorded for *Citrus* by Vanselow and Datta (1949). In the crops considered here the symptoms tended to appear and continued to be most acute in older and middle leaves until severe. Young leaves were only affected after older leaves had progressively developed severe symptoms. The young leaves and growing point thus persisted to the last, at the expense of the older leaves. In those instances where symptoms reappeared after temporary or partial recovery, older and middle leaves were again involved. These points are clearly shown from comparison of tomato plants in Plate I, Fig. b and Plate II, Fig. e. Severe effects shown in the 1950 specimens caused death of the plant, but in 1947 (Hewitt and Jones, 1947) partial recovery was associated with progressive breakdown of old leaves, while the young shoot continued to develop normally except for slight chlorosis grading into the severe symptoms below (Plate II, Fig. e). In *Citrus*, according to Vanselow and Datta (1949), symptoms also appeared in the lower (older) leaves of a particular growth cycle, but leaves that had not shown symptoms during an earlier cycle usually remained unaffected after symptoms had developed in a later cycle. Lettuce, according to Warington (1946), developed symptoms mainly in middle leaves, whilst older and young leaves were normal. In this distribution of symptoms the wide range of crops dealt with here differed in an important way from the *Brassica* crops, studied in the previous paper, where it was shown that in many types secondary effects (mainly after partial recovery) involved youngest leaves and the growing point, whilst older leaves were less affected or remained normal. This general distinction confirms that inferred by Hewitt and Jones (1947, 1949). Analyses of the foliage may indicate whether redistribution of molybdenum is achieved less readily in *Brassica* than in most other crops, when there is insufficient molybdenum for the needs of the plant. Data bearing on these points will be published separately. Preliminary analyses given by Hewitt and Jones (1949) do not allow any conclusions at present.

The wilting in pedicels of flax was analogous to that observed in pedicels of cauliflower by Hewitt and Jones (1947). The prevalence of wilting and scorch and the increase in osmotic pressures suggest that water relations are abnormal under conditions of acute molybdenum deficiency.

In spite of the varied efficiency of technique during the period of the work, it was evident that susceptibility of crops differed considerably. Thus in 1950 lettuce, sugar beet and tomato were obviously highly susceptible compared with Alsike and barley. Lettuce was comparable with many *Brassica* crops and was possibly still more sensitive than they to molybdenum deficiency. Results obtained in 1948 suggested that large seeded legumes, such as beans, were much less susceptible than

small seeded types, such as clovers. In such instances, seed reserves may materially affect the onset of deficiency symptoms. The failure to produce "scald" in beans in these experiments may have been due to seed reserves, since Wilson (1949) pointed out that the origin of the seed was often a determining factor in the incidence of the disorder. The lower efficiency of technique used in 1948 compared with that reached in later work may also have been a contributory factor, since removal of cotyledons soon after emergence did not appear to affect results appreciably. The use of seed obtained from plants grown without molybdenum would be of interest.

Although the nature of seed reserves may account in part for the difference between beans and clovers, it can hardly explain the corresponding difference in susceptibility between the clovers and *Brassica* crops, lettuce or tomato. In these crops, it must be presumed either that different concentrations of molybdenum are needed in different species to activate metabolic processes to the same extent, or that uptake under conditions of restricted supplies differs greatly between crops. Further study is needed to elucidate these problems.

In addition to certain *Brassica* crops, already discussed and reviewed by Hewitt and Jones (1952), and beans and rock melon recorded by Wilson (1949, 1949a), the main crops considered here for which there are reports of acute molybdenum deficiency in the field are tomato, sugar beet and lettuce according to Walker (1948), Wilson (1948), and Plant (unpublished). Lower-leaf scorch of flax may, according to Millikan (1948), be due to molybdenum deficiency accentuated by excess of manganese. Molybdenum has also been shown to be of economic importance in the control of Whiptail and other effects in *Brassica* crops and for nitrogen nutrition of herbage legumes in acid pastures.

The response of the clovers and lucerne shows that molybdenum is needed also by these plants when given fixed nitrogen as nitrate, independently of its importance for symbiotic nitrogen fixation. This conclusion and the typical visual symptoms induced with nitrate nitrogen are fully confirmed by the work of Warington (1950) and Evans *et al.* (1950). Anderson and Thomas (1946) found that certain herbage legumes in acid soils no longer responded to molybdenum when fixed nitrogen as ammonium sulphate or sodium nitrate was given. It was concluded by Anderson and Spencer (1950) and Hewitt (1951) that the requirements, although apparently much reduced in these circumstances, were still positive. Wilson (1949) concluded that a "scald" disease of beans in acid soils, however, was a direct molybdenum deficiency effect and not related to the nitrogen fixation process. Some crops, e.g. celery, cereals, grasses, sugar beet, showed symptoms suggestive of nitrogen deficiency when deprived of molybdenum. In others, however, the resemblance was only slight or none. Mere lack of assimilated nitrogen does not, therefore, account for the symptoms of molybdenum deficiency. Vanselow and Datta (1949) found that they could still obtain symptoms of molybdenum deficiency (though much less acute) in *Citrus* when given ammonium and nitrate nitrogen together. Hewitt (unpublished) has shown that provision of adequate nitrogen, as ammonia as well as nitrate, did not prevent acute deficiency and finally death due to lack of molybdenum in kale, rape and tomato. This finding, together with the observation by Hewitt, Agarwala and Jones (1950), and Agarwala (1951) that ascorbic acid is reduced by lack of molybdenum in all crops tested, suggests that its role in nitrate (or nitrite) assimilation may be only incidental to, although closely dependent on, a more fundamental role of the element in plant metabolism.

SUMMARY.

1. A range of crops (other than *Brassica* species) representing legumes, vegetables, cereals, grasses and others were grown in sand cultures to test their response to molybdenum deficiency.

2. Typical symptoms included grey tinting of foliage, leaf wilting, curling, withering, scorching and (in some crops only) effects suggestive of low nitrogen status. In all instances older and expanding middle leaves were affected first and showed most severe symptoms. This was in contrast to effects peculiar to *Brassica* crops noted in a previous paper.

3. Susceptibility to molybdenum deficiency varied considerably. Lettuce, tomato and sugar beet were highly susceptible and were killed in a few weeks. Clovers, lucerne and cereals were less susceptible. Grasses and large seeded legumes were generally least susceptible. In all crops tested in 1950 (where advanced technique was used) and in most tested in 1948, molybdenum deficiency reduced growth.

4. Molybdenum deficiency resulted in accumulation of nitrate in the tissues and in higher osmotic pressure in stomatal guard cells.

5. Some of the implications of relative susceptibility and of the visual symptoms are discussed in relation to the role, distribution and availability of molybdenum in crops.

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PLATE I.



FIG. (a).—Lettuce; age 33 days.
FIG. (b).—Tomato; age 60 days.
FIG. (c).—Sugar beet; age 60 days (left, control).
FIG. (d).—Sugar beet seedlings; age 34 days.

PLATE II.



FIG. (a).—Red clover leaflets (left, control).

FIG. (b).—Alsike clover leaves (left, control).

FIG. (c).—Alsike clover (left, control).

FIG. (d).—Lucerne leaves (top and bottom left, control).

FIG. (e).—Tomato (1948); deficiency symptoms in old leaves after partial recovery.

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A STUDY OF FRUIT-BUD DEVELOPMENT IN *RUBUS IDAEUS*

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A KNOWLEDGE of the time of differentiation of fruit-buds and their developmental history is of great importance in horticultural practice, particularly pruning, manuring and selection of varieties suitable for various localities.

American studies on *Rubus* have given somewhat conflicting results. MacDaniels (4) reports differentiation of fruit-buds in late January except for the Blackberries where it takes place in the autumn. Waldo (6) finds that in most varieties of *Rubus idaeus* differentiation occurs from the end of September. He considers that there is a gradient of development of buds. Both authors agree that little development of fruit-buds occurs between late November and March.

The present investigation was undertaken to find the developmental history of fruit-buds for three varieties of *Rubus idaeus* as grown in Angus. The results show that differentiation of the floral growing point is initiated in late summer and completed in spring, little development occurring during the period November to February.

MATERIALS AND METHODS.

Fruit bud development in the varieties Lloyd George (New Zealand strain), Malling Promise and Malling Landmark were investigated over a period of two growing seasons, from June, 1949, to March, 1951. The sources of material were bushes grown from canes planted in the gardens of West Park and Elmslea (Landmark, planted 1946; Lloyd George and Promise, 1949). The sites had an easterly exposure with walls to the north, south and west and a soil rated as a sandy-loam, with a pH of 7.2. The high pH, due to excess liming, had the effect of causing a deficiency in the amount of Mn ions available to the raspberries. The nitrogen content of the soil was low, and the plot received dressings of farmyard compost annually.

The buds were collected weekly for the most part. Some of the buds were dissected fresh each time, while the rest of the sample was fixed and embedded for sectioning.

FRUIT-BUD DEVELOPMENT.

General.

An account of varietal differences in fruiting time, cold resistance, etc., is given by Cadman and Wood (2) and need not be repeated here.

External stages: Dormancy.

After leaf-fall the buds are small and pointed with 5-6 bud scales showing. They increase slightly in size until the beginning of November and then come to a standstill until the middle of January when growth begins again.

In Scotland, bud-break occurs in the field towards the end of February or beginning of March in an average season. Bud-burst occurs during the latter part of March and the inflorescence is visible externally (green-bud) during April. Flowering begins towards the end of May or early in June and fruiting from end of June to middle of August, times varying with the variety.

The terms used for the stages of the bud are those given in the Ministry of Agriculture and Fisheries bulletin (5), with the additional term "break" for the stage between dormant and bud-burst.

There has been little previous study of dormancy in *Rubus*. MacDaniels (4) and Waldo (6) agree that little fruit-bud development takes place between November and March. Brierley and Landon (1) consider that in the field there is a "rest period" from mid-October to early December. They do not, however, make a clear distinction between rest-period and true dormancy.

True dormancy may be defined as a condition of suspended growth and development which is unbreakable by alteration of environmental conditions or by chemical treatment. False dormancy may be broken by alteration of environmental conditions or chemical treatment. Ordinarily plants will remain in a state of "dormancy" until increasing temperature and water supply in the spring reach the threshold necessary for active growth. If the plants are resting and not truly dormant they will respond to a higher temperature by growth (Lundegårdh (3)).

This was demonstrated on *Rubus*. Cut branches were brought into the laboratory and kept in water. Samples taken before the middle of December showed no signs of development. Samples taken on and after 20th December proceeded to develop, the times taken to reach bud-burst decreasing as shown in the graph (Fig. 1).

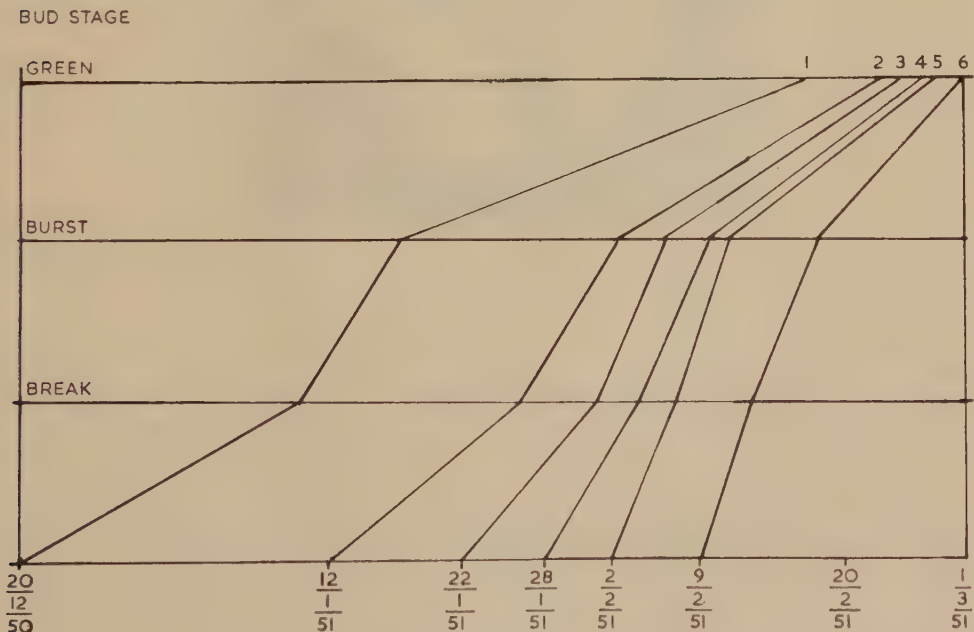


FIG. 1.

Time taken to reach various stages of opening by buds forced from given dates.

A second sample taken on 20th December was placed in the refrigerator (at approximately 30° F.) and kept there till 10th January when it was brought into the laboratory. One or two buds were removed for dissection and it was found that the inflorescences were still quite moist although the water in the container had been frozen solid and the outer bud-scales were shrivelled. Only the topmost flower had developed, a condition often found in buds exposed to low temperatures. The remainder of the buds reached bud-burst within two weeks, about half the time taken by the 20th December sample which had been in the warmth for the whole period. This rapid development is well known in the field when a warm spell



FIG. 2.

First indication of floral apex: growing point becoming flattened (11/9/49). $\times 30$.

succeeds a low temperature period. Short of complete destruction of the flower-buds, a frosty period may actually stimulate growth.

Although these experiments would require to be greatly extended to other varieties and localities, they at least suggest that the period of true dormancy is short, probably (for this area) only about six weeks from the beginning of November.

Internal development.

Flower and inflorescence. In July the bud is entirely vegetative, the growing point being rounded and producing tridentate leaves in acropetal succession. This continues throughout August and the beginning of September. Then the growing point becomes broader and flatter, this being the first recognizable sign that the apex is turning over to the production of flowers instead of leaves. Floral development is initiated in the middle of September and, by the last week, the bud

contains a definite inflorescence axis, terminated by the first-formed flower. The later-formed flower-rudiments develop basipetally in an irregular spiral.

During October development is rapid, 2-3 more flower-rudiments being produced. By the end of the month the oldest flower has far outstripped the others, showing a conical torus, 2-3 rings of anther initials and a perianth ring (see Fig. 4). The lower flowers consist of torus and perianth only (Fig. 3).

Several distinctive stages of the flower were recognized; the most striking are shown in Figs. 2-4 and are summarized in Table I.

TABLE I.
Calendar of development of the fruit-bud in Rubus idaeus.

Month.	Bud, external.	Bud, internal.	Anther.	Ovule.
September ..	Autumn bud	Floral apex recognizable		
October ..	"		1-2 rings of initial	
November ..	Winter bud	Several flowers formed	2-3 rings of initial in terminal flower	
December ..		Growth but no differentiation		
January ..	Buds swelling	"	"	Carpel rudiments
February ..	Bud-break (last week)		Anthers becoming 4-lobed	" "
March ..	Bud-burst (end of month)		Sporogenous tissue develops	Carpels enlarge and close
April ..	Green-bud (end of month)		Tapetum (1st week). Archeporium rounds off (2nd week). Meiosis in 3rd week	Nucellus and integument developing
May ..	Flowering by 2nd or 3rd week		Pollen (1st week). Ripe anthers by end of month	Megaspore in 2nd week. Mature embryo-sac by end of month

Stage I. Growing point of inflorescence axis becomes broad and flat (Fig. 2). 11th September.

Stage II. Perianth-ring beginning (Fig. 3). 29th September.

Stage III. Torus broad and flat, sepal rudiments appearing. 9th October.

Stage IV. Torus beginning to grow upwards, first cycle of anther rudiments. 16th October.

Stage V. Second cycle of anther rudiments. 23rd October.

Stage VI. Sepals turning up, 2-3 cycles of anther initials, lowest anthers beginning to show lobing (Fig. 4). 16th November.

Waldo (6) states that there appears to be a well-marked gradient of development along the cane, the buds in the middle region being the most advanced.

The writer found a similar gradient in the varieties of *Rubus* studied, in the uppermost portion of the cane. The material was taken after pruning and

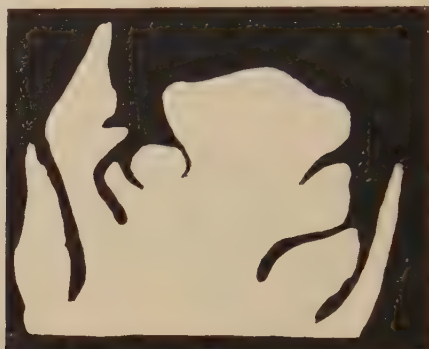


FIG. 3.
L.S. of bud (9/10/50) showing terminal flower with broad torus and perianth ring, two lower flowers torus only. $\times 15$.

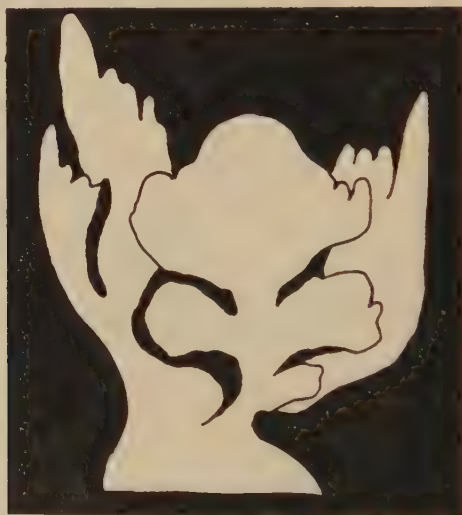


FIG. 4.
L.S. of bud (16/11/50) showing terminal flower with rounded torus, two cycles of anther rudiments and sepal rudiments. $\times 15$.

approximately one-third of the cane (counting from the top) was examined. Fifteen buds were dissected from each cane and a number of canes of each variety, cut on the same day, were used for each sample. The buds were grouped according to the flower-stage reached and three zones were recognized: zone I, buds 1-4; zone II, buds 5-10; zone III, buds 11-15. The buds in the middle zone were always the most advanced.

Lloyd George and Malling Promise showed a marked gradient, the buds in zone II reaching stage VI by the end of October or the first week in November.

Malling Landmark showed less definite zoning. Stage VI was not reached by any buds before winter, but (in contrast to the other two varieties) development continued slowly and without such a marked halt.

Throughout December and January, in all three types, the inflorescence axis lengthens and more flower-rudiments are formed. By the end of the month carpel initials are appearing in the uppermost (oldest) flower.

After bud-burst growth is suddenly speeded up, the axis lengthening so that the inflorescence, forming a small compact pyramid at the top, becomes visible in the green-bud stage. The number of flowers has increased from 5 to 7 or 8, the top three being furthest developed. The sepals now enclose the androecium and gynoecium, the petals developing just before flowering.

Anther and ovule. The stages of development in anther and ovule do not run concurrently: they are summarized in Table I. There are no special features about the development, but it may be noted that the tapetum is partly sporogenous and partly parietal in origin and that there is only one integument to the atropous ovule. There appears to be an interval of about 4 weeks between meiosis in anther and ovule.

SUMMARY AND CONCLUSIONS.

1. Differentiation of the floral growing point occurs from the middle of September onwards, development following a definite gradient in the upper third of the cane, the maximum development being in the middle of this region.

2. The inflorescence is formed in definite stages, the first-formed flower being terminal, and developing most quickly. The later ones are formed basipetally in an irregular spiral and develop more slowly. The mature inflorescence consists of 7 or 8 flowers, the top 3 or 4 being the best developed at the green-bud stage.

3. Torus, sepals and stamen rudiments are initiated before winter sets in, but further development is delayed until spring. The androecium precedes the gynoecium in maturation by about 4 weeks.

4. Development of the bud slows down in the beginning of November but, as buds can be forced after the middle of December, it seems that the period of true dormancy (if it exists) is short.

5. The results suggest that if the potential crop of flowers can be influenced by nutritional factors, manures might profitably be applied in late summer. A balance would have to be sought between the possible enhancement of flower production and the tendency to stimulate late season growth.

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AUTOTETRAPLOID GREEN WATERCRESS

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SYNOPSIS.

A tetraploid green watercress with a chromosome number of 64 was made by colchicine treatment of a commercial stock of green cress which has a chromosome number of 32. This doubling of chromosome number produces a plant with broader and thicker leaflets which, it is suggested, is a valuable feature for a salad plant. It is not, however, yet known how the new type with the doubled chromosome number will compare for yield with the original stock. Other possibilities in watercress breeding by the use of colchicine for chromosome doubling are discussed.

THE discovery in 1937 (see Fyfe, 1939) that the chromosome number of most plants could be doubled easily by colchicine treatment was hailed by some as being the start of a new era in plant breeding. It was suggested somewhat naïvely both that autotetraploids (or other types of autopolyploids), produced by doubling the chromosome number within a species, would be bigger and better plants and that allotetraploids (or other types of allopolyploids), produced by doubling the chromosome number of interspecific (or intergeneric) hybrids, would make it possible for plant breeders to combine the desirable features of the two parent species. The large amount of work which has been done on colchicine-produced polyploids (and in particular on tetraploids) during the past ten years has, however, produced so far only a few valuable new types of economic plants. It is, therefore, of some interest to consider an example of a colchicine-produced autotetraploid which, while it cannot yet be stated to be an economic success, has some promise of being so.

One reason for the failure of autotetraploids to be of any use commercially is their reduced seed fertility. Thus, in spite of selection for several years in Sweden, it has not been possible to increase the seed fertility of autotetraploid barley, although in rye (a cross-pollinated species, in contrast to the self-pollinated barley) the autotetraploid has a sufficiently high seed fertility for it to be introduced for commercial growing in Sweden (Müntzing, 1951). The low seed fertility of nearly all autotetraploids suggests first that they are most likely to be of use where the part of the plant harvested for consumption or manufacture is the vegetative organs and not the seeds or fruits, and secondly that they may be of more use in crops reproduced vegetatively. Both these conditions are fulfilled by watercress, the part sold and consumed being the leaves and stems, and vegetative reproduction being the usual method of propagation in England.

WATERCRESS TYPES.

Two types of watercress, green cress and brown cress, are grown commercially in England. Green cress belongs to the species *Nasturtium officinale* R.Br. (chromosome number, $2n = 32$) and brown cress is the interspecific hybrid *Nasturtium microphyllum* $\times$ *officinale* (chromosome number, $2n = 48$, i.e. it is triploid as compared with diploid *N. officinale*). The species *N. microphyllum* ($2n = 64$), which is common as a wild plant, is not cultivated (Howard, 1947). In both green and brown cress there are different varieties, and it is usually considered that a good variety is one which has relatively broad terminal leaflets and which tends to

maintain this desired rounded shape of leaflet throughout the year (Sansom, 1947). On being given this information verbally by Mr. C. H. Sansom prior to the publication of his bulletin, it was at once realized by the present writer that an autotetraploid watercress might be of some use, since it is well known that all (or nearly all) autotetraploids have broader leaves or leaflets than have the corresponding diploids. It was also obvious that the somewhat thicker leaflets of an autotetraploid would probably produce a more succulent type which would be advantageous in a salad plant.

COLCHICINE TECHNIQUE.

The material, of which the chromosome number was doubled, was a variety of green cress grown by Mr. C. H. Sansom in his beds at Rickmansworth, Herts., and which was considered by him to be a very good type. It had originally been obtained as seedlings from a watercress bed near Uxbridge. This bed had dried up so as to kill the original stock, and the seedlings had grown when the water returned to the bed. According to Mr. Sansom this cress had a good, green colour and comparatively round leaflets and was not free-flowering.

It appeared to be best to obtain tetraploids by doubling the original stock of the variety, rather than by first taking seed from it and doubling the seedlings, since the latter procedure might have led to some segregation of characters. The method of colchicine treatment chosen, therefore, was as follows. Five cuttings of the stock were rooted in a large seed pan standing in a saucer of water. When they were established, the plants were decapitated and drops of a 0.5 per cent. aqueous solution of colchicine were placed in the axils of the leaves so as to be in contact with the axillary meristems. One drop of the solution was given each day and the treatment was continued for four days. The plants were then left for the axillary meristems to grow into shoots. When large enough, these shoots were cut off and were rooted as cuttings, this being very easy to do in watercress since the plant normally produces adventitious roots in each leaf axil (Howard, 1940).

A total of twenty shoots from the treated axils were rooted and, of the first five to flower, three were tetraploid. They were first recognized as tetraploids by measuring pollen grain size (cf. Howard and Manton, 1946). That they were tetraploid was also confirmed by their reduced seed fertility, it being only 40 per cent. of that of the diploid. The seed from one cutting was harvested and grown to produce the autotetraploid stock. The stock of the autotetraploid (called for shortness A-4) was grown from seed in order to obtain plants free from Brassica virus 1 which is almost universal in cultivated watercress stocks (Smith, 1948). Compared with growing the diploid from seed, there should be much less segregation in the tetraploid. The chromosome number of the seedlings was counted and found to be $2n = 64$, as compared with $2n = 32$ in the diploid.

COMMERCIAL POSSIBILITIES OF THE AUTOTETRAPLOID.

Having obtained the autotetraploid, it was easy enough to see that it had, as was expected, broader and thicker leaves than the diploid from which it was produced. It also appeared, under the conditions of growth in the glasshouse, to be much less prone to flowering than the diploid. It was, however, impossible to form any opinion as to its commercial value without arranging for it to be grown in the rather

special conditions of commercial watercress beds and under the careful management which good cress growers give to their beds. Since there are no experimental watercress beds in England, it was arranged that three growers, including Mr. C. H. Sansom who had supplied the diploid stock, should be given small quantities of A-4 for bulking up and growing in their beds. One of these growers soon decided that he had no use for it since he was only interested in brown cress. The other two growers did, however, build up stocks of A-4 until they had small beds of it and the author is indebted to them for the trouble they took in this matter, particularly as he was able to supply them with only very small quantities of it (not more than enough to plant 4 square yards).

Under commercial conditions A-4 has maintained its broad and thick leaflets and has produced a very high quality cress. The differences between A-4 and the diploid from which it originated are shown very clearly in Plate I. The photographs were taken from material grown at Rickmansworth and harvested in early April, 1951. The large size and broadness of the leaflets of A-4 are very striking and made a very favourable impression on all to whom samples were given. It was also generally agreed that it was a somewhat more succulent cress to eat than the diploid.

As has been mentioned earlier, A-4 appears to be less prone to flowering than the diploid. This may make it possible for it to be cropped later in the year than the diploid. It would also be interesting to see whether it will travel better, with less wilting, in warm weather.

It is not yet known, however, how A-4 will compare in yield with the diploid, since it is only recently that a sufficient quantity of it has been available for growing under normal conditions. When gathering it, workers had the impression that it gave a somewhat thin crop as compared with the diploid, but this impression was reversed when it came to bunching, A-4 filling up chips much quicker than the diploid. The larger size of individual shoots of A-4 (see Fig. 1, Plate I), would appear to offer an obvious explanation of these two observations.

A-4 may, however, be not quite as frost-hardy as the diploid and it would also appear that the commercial success of A-4 will depend to a large extent on its resistance to "crook-root" disease (caused by *Spongospora* sp.). Like its diploid green cress parent, it will presumably be more resistant than brown cress; but it is possible that, if it grows a little slower than the diploid, it may be more susceptible than the diploid, since there are reasons (Howard and Lyon, 1950) for believing that resistance to "crook root" may depend upon the rate at which new axillary roots are produced. A-4 did remain free from the disease in the winter of 1950-51 at Rickmansworth, but so did all other green cress grown there in that winter. The lower seed fertility of A-4 may also place it at a disadvantage as compared with the diploid, since there are reasons for thinking that English growers will have to change from their present practice of propagation by vegetative means only, to growing crops from seed. Growing from seed secures young plants free from Brassica virus 1, which is widespread in watercress stocks (Smith, 1948), and appears also to give plants which have more resistance to "crook root" disease.

VITAMIN C CONTENT.

Watercress is very rich in ascorbic acid (vitamin C) and for this reason has often been advised for inclusion in diets. Since it has been suggested that tetraploid tomatoes have a higher ascorbic acid content than diploids (Crane and Zilva, 1949),

it is of some interest to know how diploid and tetraploid watercress compare. So far only a single comparison has been made. Samples from the same lots of cress from which the figures of Plate I were obtained, were tested by Dr. L. W. Mapson of the Low Temperature Research Station, Cambridge. He found that the diploid contained 66 mg. and A-4 98 mg. of ascorbic acid per 100 gm. fresh weight of the leaves. Too much reliance cannot be placed on this single determination, since it is known in tomatoes that environmental conditions can affect ascorbic acid content. On the other hand it does suggest that further determinations would be of interest.

FURTHER POSSIBILITIES IN BREEDING TETRAPLOID WATERCRESS.

It is now generally recognized that it is only exceptionally that new autotetraploids will be of immediate use and that usually they will have to be treated as initial breeding material from which valuable types can only be obtained by further breeding. So far as autotetraploid green watercress is concerned, it may be that a better type than A-4 itself could be obtained by doubling another diploid green cress stock and then crossing this with A-4.

There is, however, in watercress breeding another possibility. Brown cress must have originated at some time, presumably in wild populations, from the cross *Nasturtium microphyllum* (known only as a wild plant) $\times$ *N. officinale* (green cress). It should, therefore, be possible, as was mentioned by Howard (1947), to make a new type of cress from the cross autotetraploid *N. officinale* $\times$ *N. microphyllum*. This new type of cress would be a tetraploid with two "doses" of *N. officinale*, as compared with one "dose" in the present triploid brown cresses of commerce. This new "hybrid tetraploid" cress has been made and it has been called H-4. It is a very vigorous grower (perhaps due to the heterosis found in interspecific hybrids) but it seems that, in spite of this vigorous growth, it will be of no use commercially since it has a very pointed type of leaflet. If it were possible to find types of *N. microphyllum* with relatively round leaflets, a repetition of the cross would be worth while, since the vigour of the hybrid tetraploid would appear to be a very valuable character.

A still further possibility in watercress breeding is the production of a hexaploid by doubling the chromosome number of triploid brown cresses. This also has been done, and the hexaploid was found to have a reasonable seed fertility as compared with the very low seed fertility found in the triploid. No stock of this hexaploid has so far been grown, and it may very well be that the plant, which has a chromosome number of 96, would have too many chromosomes for it to be of any use for commercial growing, the maximum chromosome number for vigorous growth probably being the tetraploid one of 64.

SUMMARY.

Autotetraploid green watercress (known for shortness as A-4) was obtained by colchicine treatment of a commercial, green watercress variety. It has the usual features of autotetraploids and its larger, broader and thicker leaflets may make it a desirable cress for commercial growing. It also appears to flower less than does normal green cress, and this might make it possible to crop it later in the year than normally. Other possibilities in watercress breeding are discussed.

PLATE I.



FIG. 1.
Single stems of diploid watercress (left) and the tetraploid watercress, A-4 (right).



FIG. 2.
Leaves of diploid watercress (top) and of the tetraploid watercress, A-4 (bottom).
In both photographs a half-penny (diameter 1 in.) is included for a scale. Photographs by
Mr. V. Chapman.

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REVIEWS

PEACHES, APRICOTS AND OTHER STONE FRUITS. By JUSTIN BROOKE. (London: Faber & Faber. 1951. Pp. 163, illus. Price 16s.)

Mr. Justin Brooke, the widely famed grower of peaches on a commercial scale as bush trees, has already described his methods in *Peach Orchards in England*. The information in that book is now revised and directions for growing other stone fruits are added. He is a man of revolutionary ideas, but he realizes that he has little proof for many of his "large claims" and invites his reader to arm himself with a "healthy scepticism". Much that he believes and practices appears to be contrary to the evidence of sound experiments and it will be interesting to see how many of his ideas will be adopted by fruitgrowers, even on the experimental scale that he pleads for. Fourteen of the twenty-three chapters of the book deal with peaches; the development of his farm at Clopton Hall, sites, varieties, planting, cultivation, manuring, picking and marketing, the effects of severe and mild winters, pests and diseases and the utilization of unmarketable fruit. Chapters follow on nectarines, apricots, greengages, cherries and a standardized method for pruning all stone fruits. Other chapters deal with the control of Silver Leaf by bark-slitting, recommended rootstocks, and the problem of marketing small quantities of fruit. Mr. Brooke presents his ideas in an interesting and provocative way and makes one wish to try them out if only to prove him wrong. It would, however, be valuable to have figures for the crops harvested, on an acreage basis, so that the grower who has not seen Mr. Brooke's farm may judge for himself the success achieved by these methods. The book is well indexed and is illustrated by many photographs, though some of these are not very clear.

H.B.S.M.

DECIDUOUS ORCHARDS. By WILLIAM H. CHANDLER. (London: Henry Kimpton. 1951. Pp. 436. 113 figs. Price 46s. net.)

The first edition of Professor Chandler's book was a landmark in pomological literature. For almost the first time a book on growing approached the subject, not from the standpoint of practical technique, but rather from that of the physiological responses of the tree. The author expressed the opinion that the practical aspects of fruit-cultivation could best be acquired by experience on a first-class nursery and that the function of a college text-book should be rather to provide the skeleton of an orderly, detailed system of knowledge about trees, as a basis for a course aimed at explaining the underlying problems of tree behaviour. In this endeavour the author succeeded most admirably.

On his retirement from the Professorship of Horticulture in the University of California, Professor Chandler has found time to revise and bring up to date his text-book, making it even more valuable. While the greater part of the text is unchanged there has been extensive rearrangement of the sections, particularly the first half, which deals with all aspects of tree growth and development in general. Certain subjects have been rewritten in the light of recent research, especially where hormone mechanisms are involved, and a list of 272 recent papers, published since the first edition, has been added.

A great virtue of the book is that, unusually for an American text-book, work

in this country receives as much attention as that of the U.S.A. The book is, therefore, of the utmost value to British students and should become the standard work on scientific pomology. It is unfortunate that, in spite of a small reduction in size, the cost is more than double that of the original edition. R.H.S.

A HISTORY OF HORTICULTURE IN AMERICA UP TO 1860. By U. P. HEDRICK. (New York: Oxford University Press. 1950. \$7.50.)

Books which treat horticultural history as an integral part of either economic or what is now called "cultural" history have become decidedly rare. Yet— notwithstanding the *Dictionary of National Biography's* inexcusably many omissions from the ranks of British pomologists, plant-hunters, plant-breeders and other botanical pioneers—the growing importance of horticulture's role in our national history cannot be seriously disputed. If books like the so pleasantly readable and richly informative one under review are now seldom published over here, our own horticultural experts, whose business it should be to compile them, must take their share of the blame. Judged by the increasingly esoteric jargon they frequently write in, which, though doubtless lucidity itself to their professional colleagues, is only too effective in warning off the common reader, more and more of them seem anxious to be regarded as purely "specialist" authors with all the self-imposed restriction that the term implies.

A nation with a short history can be trusted to preserve the data of its achievements all the more eagerly and piously. Students of development of horticulture in Britain will be filled with envious admiration for the wealth of accessible documentation Mr. Hedrick was able to draw upon. Of how many older named English varieties of fruit can we say with any degree of certainty by whom, when and where they were raised or introduced? Mr. Hedrick can give the answer in the case of virtually every American-bred apple, pear, quince, plum, cherry, vine, raspberry, blackberry and strawberry which at one time or another was grown or known in Europe, besides the legions of those that were not. This alone lends an added interest to his book for the layman, and tells him far, far more besides. He will learn just what strange fruits and other useful or decorative plants the first colonists of North America found growing there and, later on, cultivated or improved; which kinds they imported from Europe; and to what extent they developed species native to the Old World and subsequently hybridized them with those of the New. Thus, in spite of a wealth of indigenous vines, for three centuries the settlers continued to scorn native grapes, and strove to domesticate the European vine, which obstinately refused to thrive in the Eastern States. It was not until the appearance of "Concord", in 1850, that grape-growing became of commercial importance in the United States.

In "The Indian Gardens", perhaps the most fascinating chapter of all, Mr. Hedrick carefully winnows the incontrovertible basic facts of what he calls "pre-settlement" Indian agriculture from the often highly fanciful accounts left us by early explorers. Such tribes as did till the soil were by no means primitive cultivators. Thus, long before the arrival of the English, the Indians were growing "kidney beans, which they trained on poles". Between their bean or maize rows the Indian gardeners grew native pumpkins and squashes in precisely the same way that American farmers have grown them ever since. A simple way of forcing pumpkin plants had been discovered by them: the seeds were sown in bark boxes

filled with powdery decayed wood which were kept suspended in the smoke of the wigwam fires ; within a few days they germinated and, soon after, the young plants could be pricked out and planted. Their principal vegetable was the Jerusalem artichoke—which probably originated west of the Mississippi. "Potatoes were the least of root crops till the middle of the 17th Century" for the Indians found artichokes much easier to grow. Such as they did have were most likely a form of sweet potato, as the true white-fleshed Spanish type had then to be imported from Bermuda.

Long before the appearance of the white man the Iroquois and Hurons had acquired a much envied reputation as tobacco-growers and were actively bartering this produce with other tribes.

The inaugural date of American horticulture was 7th March, 1621 when, the first terrible winter being over, the Pilgrims could at last sow in the soil of their New England "the garden seeds" they had brought from home. But farther south, in Mexico and Florida, the Spaniards had long before introduced cucumbers (as early as 1494), water melons and peaches. Peach trees spread rapidly northwards from Texas and became so widespread that the first botanists to visit the New World believed them to be of American origin. All the North American apples or pears originate from seeds brought from Europe. The first orchard, which was still bearing well in 1765, was planted by the Rev. William Blackstone in Boston somewhere about 1630 ; and as early as 1648 a Connecticut nurseryman could offer native-grown apple trees of old Norfolk varieties like Belle Bonne. Swaar, which the Dutch Shakers were growing on the Hudson before 1700, would seem to be the oldest named American apple. But Green Newtown Pippin must have been raised in Long Island considerably earlier than 1759, for even before the War of Independence it was being regularly imported in "strawhead barrels" costing a dollar to a dollar and a half apiece. Not even Mr. Hedrick can account for the cryptic name of Northern Spy which dates from about 1800. Up till 1825, or thereabouts, commercial orchards were planted solely for making cider, of which there was an enormous consumption. It was in 1860 that "The Father of American Apple-Breeding", Peter Gideon of Minnesota, crossed an ordinary apple with *Malus baccata* and thereby produced Wealthy.

However, the first settlers found, or could have found, an abundance of bilberries and cranberries, besides a profusion of wild plums, vines, *Rubus* fruits, gooseberries, currants and strawberries, all of which belonged to species unknown in Europe. The 11 species of native plum are now represented by 433 pure-bred and 155 hybrid varieties ; the four species of American raspberry and six of American blackberry have in course of time produced 280 and 23 varieties respectively.

Like the European vine, the European gooseberry refused to thrive. *Fragaria virginiana*, the native strawberry from the marriage of which with *Fragaria chiloensis* all large-fruited strawberries are supposed to be derived, was not brought into cultivation till the end of the eighteenth century. Hovey, the first deliberate cross in America and the first variety of commercial importance there, dates from about 1838. This was succeeded in 1854 by Wilson, which enjoyed the longest run of any American strawberry. Its breeder, James Wilson of Albany, N.Y., also raised (or more probably selected from wild canes) the first American raspberry to be given a name. Nor must we forget that the Americans raised some of the very finest-flavoured European (*Prunus domestica*) plums there are ; Washington (a very

shy bearer over here) dates from 1790, and Joseph Cooper (our Cooper's Large or Lady Lucy, or La Délicieuse of France) a decade or so later. Judge Buel of Albany, N.Y. (where Denniston's Superb also originated) raised Jefferson about 1825; the date of McLaughlin's Gage, which hails from Maine, is 1840.

Why, with such an extraordinary abundance of wild and cultivated fruits, the United States should have been the first country to embark on the commercial growing of blackberries and dewberries, which began there about 1835, is by no means clear. In any case, the commercial cultivation of cranberries and bilberries (blueberries) had started much earlier, whereas the breeding of tomatoes only began seriously in 1850. As to American pears, if we can assume that the Bartlett is our Williams', almost the only varieties that at one time or another have found favour on this side of the Atlantic are the delicious little Seckel, a wilding found near Philadelphia before the Revolution, Dana's Hovey (1854) (which, with all due respect to Mr. Hedrick, as grown over here is certainly not "the most delectable of pears"), and the great, gritty Clapp's Favourite (1860) that likewise hails from Massachusetts.

P.M.S.

RECENT ADVANCES IN THE STUDY OF PLANT VIRUSES. By KENNETH M. SMITH. (London: J. & A. Churchill, Ltd. 2nd Edn., 1951. Pp. 300, illus. Price 22s. 6d.)

This is a very useful book for the student of plant viruses, as it covers the entire field of research in its diverse aspects. Plant virus research has greatly changed since the first edition was published in 1933, and even the general format is altered in this second edition, with new chapters on electron microscopy and on serology. Subjects covered in the first edition have been rearranged so that they fall logically under the chapter headings: Symptomatology; Physiology of diseased plants; Insects in relation to viruses; Methods of transmission; Methods of purification; Properties of purified viruses; The sizes of viruses; Strains, mutations and variation in viruses; Control of plant viruses; Classification and nomenclature.

These chapters are not equally comprehensive, however; those on aspects in which the author and his collaborators in research have been most active in recent years contain very full discussions and are followed by more up-to-date bibliographies than are other chapters. If references to publications after 1947 are considered (the title is *Recent Advances*), we find that the three chapters on electron microscopy, serology and control, classification and nomenclature have twenty-four, while the remaining eight chapters (excluding the introduction) have only fourteen different references. The choice of references seems odd in some instances. Why, for example, should a reference to cacao viruses in Trinidad be cited in relation to swollen shoot disease in West Africa, and yet recent papers on the subject be omitted from the bibliography?

The bibliography is, perhaps, the weakest part of this book, in view of the emphasis in the title on recent research. To students and research workers a valuable attribute of the book is the description of methods employed in the different techniques. These accounts are sometimes sufficiently detailed to be followed without reference to original papers, so that this book, with its other assets of clear text and excellent photographs, is an invaluable textbook for the virus laboratory.

A.F.P.

NATIVE ORCHIDS OF NORTH AMERICA. By D. S. CORRELL. (London : Wm. Dawson. Mass : Chronica Botanica Co., Waltham. 1951. Pp. 399, bibl. 137, illus. Price \$7.50.)

In view of the large and detailed monographs which have been published dealing with the orchids of Europe, a comprehensive treatment of those of the North American continent is long overdue. The appearance of Dr. Correll's very attractive book is, therefore, all the more welcome. The author was for many years associated with the late Professor Oakes Ames, whose knowledge of American orchids was unrivalled, and this association is reflected in the excellence of the present work.

The orchids of North America, about 200 species in all, include a number which are popular rock- or bog-garden plants, such as the various Lady's Slippers, but there are many other hardy species which would be well worth cultivating. In addition to the hardy species, which are mostly terrestrial plants, there are some tropical or sub-tropical species restricted to the southern parts of the United States, especially Florida. These would require greenhouse cultivation, and include a number of epiphytic species, many of them very striking.

Following a short introductory chapter, the main part of the book consists of a systematic account of the various genera and species of orchids occurring in the United States and Canada, with well-designed and easily used keys for their identification. There are excellent but simple descriptions of each, while almost all the species are accurately portrayed by nearly 150 charming line drawings. Dr. Correll adopts on the whole a conservative attitude as regards both genera and species, and this must be taken into account in making detailed comparisons with European orchid treatises.

Information regarding natural habitats and geographical distribution is added, together with notes on pollination, variation, hybridization and other biological features in many cases. Professor E. T. Wherry and Mr. J. V. Watkins have supplied for each species very useful notes on cultivation, which will be of special interest to horticulturists. A glossary and selected bibliography of publications on American orchids complete the text. The book is clearly and tastefully printed, and is indeed a model of what such a book should be. It will undoubtedly remain the standard work of reference on this subject for many years.

V.S.S.

THE DESIGN OF EXPERIMENTS. By R. A. FISHER. (London : Oliver and Boyd. Sixth Edition, 1951. Pp. 242. Price 12s. 6d.)

It is now sixteen years since this fine book first appeared and neither familiarity nor the passage of time dulls its lustre. Indeed, the more it is read the greater its wisdom appears, while the ever increasing complexity of techniques makes its enunciation of first principles more and more necessary. With students it has the reputation of being difficult, but this criticism arises from misunderstanding and a narrowness of vision. It does not set out to provide instruction about useful experimental designs, interspersing the descriptions with general comments, but rather to declare general principles and to illustrate them with a diversity of examples, some of them calling for quite specialized knowledge. Its achievement lies in the width of its survey and those who are troubled by the intricacies of some of the examples need not be dismayed if they have understood the principles.

S.C.P.

THE NEW CHRYSANTHEMUM TREASURY. By J. H. GODDARD. (London : W. H. & L. Collingridge Ltd. 1951. Pp. 256, illus. Price 15s.)

The New Chrysanthemum Treasury by J. H. Goddard is pleasantly written by an amateur of some considerable experience in growing for exhibition, and the chapters dealing with exhibiting and staging are full of useful information. Mr. Goddard amply demonstrates his skill as a judge in offering ten pages of useful hints. The book contains 8 excellent colour photographs and 91 clear pictorial half-tones.

Societies could benefit from the author's suggestion that their shows are worthy of more than one day's duration; it is true that the members rarely appreciate the immense work executed by the chief officers of these societies.

It is unfortunate that the author has not given to chrysanthemum cultivation the attention which the subject deserves. From a total of 256 pages, 102 are devoted to the classification of varieties, approximately 600 of them. While this is of immense value as a reference, it will present an enormous headache to the beginner. When will "literary-growers" learn to limit their recommendations?

The little cultural information, while offered in a pleasant friendly fashion, contains too much padding and could have been provided in about one-third of the space, and the General Index which is contained in two pages, gives an indication of the scanty factual information.

Some stopping dates are provided and these serve as a useful guide, but no reference is made to "natural breaks", and the term "pinching" is not commendable.

No reference is made to the production of selected stock plants, a feature which ought to be of importance to the amateur, and Chapter III causes confusion in not indicating the types referred to in the cultural notes.

Important omissions are the quantities of chalk, fertilizer, insecticides, etc., which should be used. An amateur requires strict guidance on these points and it is confusing to have complicated composts suggested for one operation, and John Innes composts for another. While appreciating the difficulty of steam sterilization for the amateur, at least it would simplify his lot to be given, say, J.I. 1 for cuttings, J.I. 2 for 60's, J.I. 3 for 48's and J.I. 4 for 16's. An example of this confusion is offered on p. 35 when J.I. 3 is discussed in conjunction with potsful and barrow-loads of ingredients, and the mixture of soot and lime is not to be recommended.

Feeding would be advisable up to the time of cutting the blooms and should not stop when plants are housed. There is no mention of disbudding of mid-seasons before housing, and the scant attention paid to Bishop Bug is surprising. In controlling pests, little importance is given to D.D.T. and amateurs would be better advised to use B.H.C. rather than H.E.T.P.

It is evident that much fuss must be made in producing pot-grown varieties but the impression is given that early-flowering varieties can be grown on almost any kind of soil and with but meagre cultivation.

While undoubtedly the author's chief love is the production of flowers for exhibition, *The Chrysanthemum Treasury* would have been of greater value if some information had been given on the growing of pot chrysanthemums suitable for indoor decoration and, while specimen plants are illustrated, no mention of them is made in the text.

The book is expensive at 15s., but no doubt the inclusion of the colour plates has influenced its price.

J.H.

BEANS. (Ministry of Agriculture, London, Bulletin 87, Second edition, 1950. Pp. 35, illus. Price 2s.)

This bulletin deals separately with the cultivation of the three main types of culinary bean grown commercially in England; the broad bean, the French bean and the runner bean. Beans grown for stock-feeding are not included. Since the first edition in 1935, the material has been considerably revised and rearranged. The somewhat complicated section on varieties of French beans, for instance, has been simplified by the omission of the stringless and waxpod varieties, which are little grown in this country, and by the transfer of information on climbing varieties to the section headed "French beans under glass". The section on beans for canning and harvesting dry contains more specific information on cultivation and harvesting than in the previous edition, while that on pests and diseases has been extended.

A useful appendix has been added on local practices in runner bean production in Worcestershire, one of the largest producing areas. It is interesting to note that in the Bromsgrove district the seed is sown by being pushed into the ground with the fingers. The two new plates, showing Worcestershire methods of staking and irrigation, are not very clear. P.R-D.

FRUIT CULTIVATION FOR AMATEURS. By HILARY HUGHES. (London: W. H. & L. Collingridge Ltd. 1951. Pp. 477, illus. Price 25s.)

This is a comprehensive and up-to-date guide and reference work on fruit-growing for the keen amateur. It is divided into three parts dealing with general methods, hardy fruits described alphabetically, and fruits under glass; the work is adequately indexed and includes a separate index for pests, diseases, and functional disorders. The numerous plates reach a very high standard indeed.

The reader will find in this volume up-to-date information from the reports and journals of English research institutes condensed in a very clear style. Plans are given of the Bradbourne (East Malling) and Wisley model fruit gardens, while the owner of an old established garden will find all he needs concerning the improvement of neglected trees, frameworking, and pest and disease control. One chapter is devoted to the amateur propagator and another gives many useful hints which will be of value to those exhibiting their fruit either locally or in London. Miss Hughes has sought the advice of a barrister-at-law on such legal points as the removal of fruit trees on terminating a tenancy, the overhanging fruit tree and "next door's" suckers. These and other points are set out in question and answer form and make a novel addition to a fruit-growing handbook. The special requirements of individual fruits are mentioned in detail and a chapter is included on outdoor grape vine culture, based largely on the recent results from the Oxted Viticultural Research Station in Surrey.

A few parts of the book may need revision in a second edition. The explanation of the terms "notching" and "nicking" on pages 117 and 118 seems confused. The reviewer would like to see a spring Bordeaux mixture spray recommended in addition to the autumn one for bacterial canker control on cherry, since recent work has shown the necessity for both sprays to ensure adequate control of this disease. It is recommended that after planting a fruit tree the final level of the soil should be just *below* the *graft union*, but in view of the serious risk of scion rooting it would surely be preferable to allow several inches between soil level and the union; this

is of especial importance to the amateur who has selected his rootstock carefully and has closely planted trained trees. On checking excessive vigour (p. 146) the statement that "the aim of ringing is to check the uptake of water and nitrogenous food from the roots" seems an error. With well pruned and adequately manured trees it is assumed that fruit thinning of apples will not be necessary, although Miss Hughes recognizes that with a very heavy set it is best to thin as soon as possible, as the remaining fruits are then less likely to drop off in the "June drop" (p. 192)—but, since "singling" or very light thinning has been shown experimentally to have little or no effect on subsequent "June drop", some guidance as to degree of thinning seems necessary here.

Miss Hughes and her publishers are to be congratulated on producing a very fine work for the amateur fruit enthusiast. A.P.P.

CAMPANULAS. By H. CLIFFORD CROOK. (London: Country Life Ltd. 1951. Pp. 256, illus. Price 35s.)

The recent Country Life publication *Campanulas* by Mr. Clifford Crook will be warmly welcomed by all who are interested in this very large and complicated genus. Hitherto, identification of the species has been a matter of considerable difficulty for the gardener, owing to the existence of innumerable synonyms and the lack of detailed description. Mr. Crook has set out to record every known species in the world, and has compiled his descriptions, wherever possible, from a first-hand study of the living material. The text is illustrated by 216 photographs in monotone of the high standard we have learnt to expect from Country Life publications.

This is the first comprehensive study of the Genus *Campanula* to be published since the French botanist Alphonse De Candolle brought out his *Monographie des Campanulacées* in 1830, and it contains descriptions of many plants discovered since that date. It does not include a key, but one chapter deals with classification and indicates the lines which this should follow. The main part of the book gives detailed descriptions in alphabetical order of the majority of the species which are known. Many species are extremely similar and possibly the differences are merely geographical. The names which have been used by the "Splitter" group are given in Chapter V, together with the reasons for grouping them. The descriptive matter is clearly and concisely written, and no one should have any difficulty in deciding which species they are concerned with.

There is a chapter dealing with cultural matters, which outlines the chief methods of propagation and cultivation. This is particularly valuable for those who grow the more difficult species. Another chapter is devoted to hybridization, and from this we learn that only a few species can be hybridized with any success, most species apparently being incompatible with one another. This, it is stated, is surprising in a genus of this enormous size, where the species overlap to a considerable extent. The Appendix consists mainly of a list of synonyms, both of the species and of the closely related genera, thus removing much of the confusion which has existed in the past. Four additional species of which information has been obtained since the list was compiled are described in the Addenda.

Besides making constant reference to the work of De Candolle, reference is also made to the Botanical Magazine, the Index Kewensis, and to Linnaeus Farrer, Dr. Guiseppi, Sampson Clay, Col. Beddome and T. Ingwersen, among others; where the plant has been given an Award of Merit, the year in which the award was made

is stated. The country of origin is mentioned and also whether the plant is of annual, biennial or perennial duration.

Mr. Clifford Crook has spent over thirty years collecting the material for his book, and has travelled widely to obtain his information. He has provided us with a valuable extension of horticultural knowledge and all who are interested in plant collections will do well to have this book at hand for constant reference.

M.P.

BASIC HORTICULTURE. By V. R. GARDNER. (New York: The Macmillan Co. Revised ed. 1951. Pp. x + 465, illus. Price 36s.)

A British teacher of horticulture compiling a list of books to recommend to his students gets on nicely until he comes to the general textbooks, then he finds that there is no comprehensive book that successfully unites horticulture with the sciences on which it so largely depends. With a feeling of disappointment, he turns to books by American authors and usually finds that they are so characteristically American as to be quite unsuitable for inclusion in his list. *Basic Horticulture* is perhaps the exception and it deserves careful consideration because its emphasis is on fundamental science and its interpretation with horticultural practice. The author has set himself the task of assisting the student to acquire a knowledge of the structure and development of many kinds of fruits, vegetables and ornamental plants and an understanding of how plants react to different environments. He points out in his preface that the factual information and the material he has selected represents his personal selection and another teacher would naturally select other material and examples. Nevertheless Dr. Gardner's scheme has much to recommend it and with little modification would suit the needs of students in any country.

The book contains twenty-three chapters, and perusal of the chapter headings in the table of contents shows how the author has treated his subject. He first defines horticulture and shows how it maintains its place in American agriculture and contributes a little over a third by weight of the constituents of recognized desirable diets. The classification of plants is next considered, then plant structure and growth, and the specialized forms of buds and stems that are of particular importance in horticulture.

Four chapters are then devoted respectively to temperature relations of plants, water as a limiting factor, light and plant nutrients. This section is well presented, the examples are of general interest and most students of horticulture would find here much that would help them in their studies.

Following these preparatory chapters are others dealing with various aspects of water and nutrient intake, carbohydrate synthesis and utilization, growth and tissue differentiation, leading finally to flower bud formation and flowering and fruiting habits.

Upon this broad scientific foundation Dr. Gardner builds his more horticultural applications. He covers pruning and the training of plants and trees in practice. He describes in considerable detail many aspects of propagation, and the uses of growth-regulating substances and the control of plant growth as exercised in routine practice in the many sections of specialized horticulture. In the last group of chapters he describes the growing of annuals, biennials and perennials and emphasizes throughout the application of the scientific principles he has already discussed. He concludes with three chapters on the protection of plants from pests and diseases and from

weeds. In these chapters he cites American examples but the principles of control are sufficiently clear to enable the reader, who already has some knowledge of the subject, to recognize them and make substitutions to suit himself.

Like many American textbooks, each chapter ends with a list of relevant problems. Here is one taken at random from p. 393. "How would you tell whether the small size of an apple or pear tree, obviously very small for its age, was due to a dwarfing stock, drought, lack of soil nutrients, high water table, or a fungus infection of the roots?"

There is an up-to-date glossary and an adequate, but by no means comprehensive, index. For instance the glossary tells us that "Pelleting = treatment in which a seed is embedded in a matrix resulting in a small hard ball" but "pelleting" does not appear in the index, though it is described in some detail on p. 328.

The book is well produced, the photographic illustrations are clear and helpful and the print easy to read.

Though it is unfortunate for readers in Britain that there is no bibliography, the book is yet one of the most up to date and comprehensive of its kind.

H.W.M.

PANSIES AND VIOLAS FOR EXHIBITION AND GARDEN. By H. H. CRANE.
(London: Collingridge. 1951. Pp. 101, illus. Price 8s. 6d.)

This little book makes a timely and welcome appearance at a moment when popular interest in the pansy and viola shows definite signs of revival. Literature by competent authority, covering the whole subject, is scarce and many years out of date. In the course of two world wars and the difficult years between, many attractive varieties have disappeared. The exhibition pansy with the rigid show bench rules of form, colour and texture to which it had to conform has probably gone for good; for the time, trouble and concentration needed to produce such geometrical wonders is not to the taste of these impatient days. Choice now falls on the massed colour of bedding varieties rather than on the perfection of the solitary bloom. Though some have fallen by the wayside, a fair number of useful bedding sorts remain and these are given full attention here. A very complete account, in small compass, of the propagation of all types of pansy and viola has been provided and this includes hybridization and the raising of new varieties from seed. The need for discarding all but the very best is stressed, for inferior types are becoming increasingly prevalent. The historical notes in chapter I are of more than passing interest.

G.StC.F.

PRINCIPLES OF PLANT INFECTION. By ERNST GÄUMANN. (London: Crosby Lockwood & Son, Ltd. 1950. Pp. 543, illus. Price 63s.)

The first edition of *Pflanzliche Infektionslehre* (Basel, Switzerland, 1946) was hailed by Professor William Brierley, who is chiefly responsible for the present version in English, as "a notable landmark in the development of the subject" of plant pathology. It is, he suggests, the first serious attempt to weld "the increasing aggregate of data, techniques, and expertise on plant diseases" into a coherent and comprehensive theory and, as such, "marks a long and decisive step towards the establishment of plant pathology as a science".

The background to the present work is provided by the author's two preceding *magna opera*, his *Comparative Morphology of the Fungi* (1926), which deals with the

pathogenic fungi *in vacuo* so to speak, and his *Biology of the Plant Parasitizing Fungi* (1929) written in collaboration with Professor Edward Fischer of Bern, which also deals with these pathogens *qua fungi*, but this time in their host plants. In the present work, the final member of the trilogy, the pathogenic organism and the host are considered solely *in mutual relation* and the unit of reference here is therefore the pathogen-host-environment complex considered in all its multifarious aspects. These are treated in a sequence of six chapters, or sub-treatises, corresponding to the six fundamental questions common to both medicine and plant pathology. The first four deal with the four pre-requisites for the successful establishment of any parasitic disease, namely, the penetration of the host by the pathogen (Chapter 1), the access of the pathogen to the host (Chapter 2), the adaptation of the pathogen to the host (Chapter 3), the proneness of the host to attack by the pathogen (Chapter 4). Finally, Chapter 5 deals with the manifestations of this positive relationship (i.e. the symptoms of the disease) and a comparatively brief Chapter 6 with the problem of combating it (i.e. with the principles underlying control measures).

It would be impossible in a brief review adequately to convey a conception of the scope, in analytical completeness and rich content, of the discussions under each of these main headings (an excellent synopsis is provided as a preparatory table of contents) or of the wealth, in range and depth, of the illustrative material which is marshalled at every turn of the argument. The whole field of known parasitic diseases of plants is freely culled, and at every stage the analogies, real and false, between plant pathology and human medicine are noted and critically examined. Thus, to take random examples, in the Introduction the differing character of advances in these two sciences is related to the wider field of reference comprehended by plant pathology, and to the greater emphasis on the diseased individual in human medicine. The mode of quoting specific plant diseases may be illustrated by the fact that the total of nineteen citations of Apple Scab occur through all the five principal chapters of the work.

Enough has perhaps now been said to show that this work is far other than a text book, or catalogue, of discrete plant diseases. What it does provide for the first time is a common approach, or theory, for the study of any one of these disparate diseases, or groups of diseases, and as such must surely find a place in the syllabus of reading required in any future course of training in plant pathology.

In his admirably produced English version, Professor Brierley has been well served by his team of translators, Miss Kathleen Secker, Mrs. F. L. Balfour Brown, Dr. Joan Moore, and Dr. W. W. Schabe, and, in the final stages of producing an homogenous text, by his wife, Dr. Marjorie F. Brierley. Corrected proofs were read by the author, whose emendations were incorporated. There is a list of references to the cited literature, an appendix giving the United Kingdom and United States equivalents of variant names of host plants and pathogens used by the author, and a good index.

R.V.H.

PUBLICATION RECEIVED.

GUIDE TO THE NATIONAL PINETUM AND FOREST PLOTS AT BEDGE-BURY. (Forestry Commission. H.M.S.O. 1951. Pp. 65, illus. Price 2s. 6d.)

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